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Preliminary studies on a mandibulohyoid 'ligament' and other intrabuccal connective tissue linkages in cirrhitid, latrid and cheilodactylid fishes (Perciformes : Cirrhitoidei)
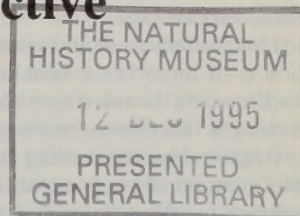
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CONTENTS

SYNOPSIS. In certain taxa of at least three groups of percomorph fishes belonging to the cirrhitoid families Cirrhitidae and Latridae, there is a connective tissue linkage between the mandible and the hyoid arch, suggestive of the mandibulohyoid ligament described in certain sub-percomorph groups. This ligament is generally thought to be a feature of lower teleost fishes, although a mandibulohyoid connection has also been identified in a few more derived taxa. The mandibulohyoid connection in the Cirrhitidae examined would appear to originate from the tendinous aponeurosis associated with the Aw division of the adductor mandibulae muscles, but its derivation in the latrid species *Acantholatris monodactylus* remains undetermined. The Aw aponeurosis in *A. monodactylus*, as well as in the latrid *Mendosoma*, and in two genera of Cheilodactylidae (*viz. Chirodactylus* and *Cheilodactylus*) ramifies extensively over the paladoquadrate arch and part of the opercular series. This system, together with various intrabuccal ligaments is described from representatives of the three cirrhitoid families studied.

It is concluded that, contrary to several earlier ideas, a mandibulohyoid linkage is of taxonomically and phylogenetically widespread occurrence in teleosts but that it might be derived from different connective tissue sources. The value of this connective tissue complex in phylogenetic studies has yet to be established, but it appears to be of use in at least establishing intragroup relationships within the Cirrhitoidei.

INTRODUCTION

A recent anatomical study of certain cirrhitoid fishes (*sensu* Greenwood, 1995) has revealed a number of markedly different ligament and tendon systems which separately or conjointly link the mandible with the hyoid arch, the palatoquadrate arch and the opercular series. Some of these connections have a degree of complexity not previously recorded among teleost fishes.

Of particular functional interest are the two types of direct and ligament-like connections between the ceratohyal and mandible in some cirrhitid species, and a third type found in one of the latrid species examined (family placement after Greenwood, 1995). These linkages invite comparison with the so-called mandibulohyoid ligament generally thought to be commoner in lower teleosts than in perciform taxa, or even restricted to the former groups (see Verraes, 1977; Lauder & Liem, 1980; Lauder, 1982; but see also Osse, 1969, Springer *et al*, 1977, and Aerts *et al*., 1987 for certain perciforms, and Anker, 1974, for gasterosteiforms). A mandibulohyoid ligament also occurs in the semionotiform lepisosteids *Lepisosteus* and *Atractosteus* (Wiley, 1976).

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† Dr Greenwood died 3 March 1995.

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The nature of the hyoid-mandibular connection in the cirrhitoids, a derived percomorph group (Greenwood, 1995), and that described in other teleosts and in the Lepisosteidae, raises doubts about the strict homology of the connection in these various taxa.

Functionally, it would seem that a mandibulohyoid connection is of importance both in adults (see Aerts *et al.*, 1987) and in early larval stages (Verraes, 1977); its phylogenetic history in this context is discussed at length by Lauder (1982).

Regrettably, the feeding studies on cirrhitoids, from which this anatomical study arose, are not sufficiently advanced or refined to allow informed speculation on any correlation between the morphology and the feeding habits of these fishes. Furthermore, many other cirrhitoid taxa remain to be studied before it will be possible to evaluate what significance the different types of intragroup mandibulohyoid and other linkages (or absence thereof) may have in unravelling the taxonomy and phyletic relationships of the group. Nevertheless, there are indications from this study, and from information in the literature on various forms of mandibulohyoid connections, that further investigations may yield insight into the biomechanics of feeding and into historical relationships.

MATERIALS AND METHODS

Material

Clupeidae: *Etrumeus terres*. RUSI 34140 (1 specimen)
Salmonidae: *Oncorhynchus mykiss* RUSI 36417 (3 specimens)
Characidae: *Hydrocynus vittatus* RUSI 19355 (1 specimen)
Cirrhitidae: *Amblycirrhitus bimacula* RUSI 77–20 (3 specimens)
Cirrhitichthys oxycephalus RUSI 40526 (3 specimens)
Cirrhitops fasciatus RUSI 2375 (1 specimen; *ex* Hawaii)
Cyprinocirrhites polyactis RUSI 12339 (3 specimens)
Paracirrhites arcatus RUSI 30975 (2 specimens)
Paracirrhites forsteri RUSI 39419 (3 specimens)
Latridae: *Acantholatris monodactylus* RUSI 33485 (2 specimens)
Mendosoma lineatum
RUSI 33613 (1 specimen)
RUSI 33626 (1 specimen)
RUSI 26176 (1 specimen)
Cheilodactylidae: *Cheilodactylus fasciatus* DIFS unreg. (2 specimens)
Cheilodactylus pixi DIFS unreg. (3 specimens)
Chirodactylus brachydactylus DIFS unreg. (3 specimens)

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Method

The entire opercular series, palatopterygoid arch and hyoid arch of one side, together with the mandible, premaxilla and maxilla of that side, were dissected away from the head. Muscles, tendons and ligaments were examined on the dissected side, and checked on the contralateral aspect which was left *in situ*.

All specimens had been fixed in formalin and preserved in either ethyl or propyl alcohol.

In the absence of ontogenetical information on the development of ligamentous and tendinous systems in these fishes, ligaments and tendons in the various taxa are presumed to be homologous if their places of origin and insertion are similar.

ABBREVIATIONS FOR FIGURES

Abbreviations for tendons and ligaments are given separately with each figure.

Muscles:

Add. mand.
I u & m: Adductor mandibulae A_1 upper and main divisions respectively
Aw: Aw division of adductor mandibulae muscle
Awt: Tendinous aponeurosis of adductor mandibulae Aw
Geh: Geniohyoideus
Im: Intermandibularis
St: Sternohyoideus

Skeletal elements:

Ang: Anguloarticular
Bb: 1st basibranchial
Ch: Ceratohyal
Dt: Dentary
Ect: Ectopterygoid
Ent: Entopterygoid
Epi: Epihyal
F: Raised facet for articulation with epihyal
Ga: Gill arch
Hyom: Hyomandibula
Hyp: Hypohyals
Ihyl: Interhyal
Iop: Interoperculum
Max: Maxilla
Mt: Metapterygoid
Pal: Palatine
Pop: Preoperculum
Q: Quadrate
R: Retroarticular
Sy: Symplectic
V: Vomer

LIGAMENTOUS AND OTHER CONNECTIVE TISSUE LINKAGES BETWEEN THE MANDIBLE, THE PALATOQUADRATE, THE HYOID ARCH, AND THE OPERULAR SERIES IN THREE CIRRHITOID FAMILIES

The family Cirrhitidae

On the basis of their mandibulohyoid connections, two distinct groups can be recognised within the cirrhitid species examined. A third group, represented by *Amblycirrhitus bimacula* (Jenkins), has no macroscopically detectable mandibulohyoid linkage (see below).

Group I species (*viz. Cyprinocirrhites polyactis* [Bleeker], *Cirrhitichthys oxycephalus* [Bleeker] and *Cirrhitops fasciatus* [Bennett] have a stout, ligament-like connection between the ceratohyal of each side and the coronoid process of the corresponding dentary ramus (Fig. 1A). Group II species (*viz. Paracirrhites arcatus* [Cuvier] and *P. forsteri* [Schneider] also have a ligament-like band of tissue stemming from the lateral aspect of each ceratohyal, but here it links each hyoid arch with, predominantly, the corresponding quadrate, on which it inserts immediately above that bone's process for articulation with the anguloarticular. Part of this tissue, however, is apparently continous with the tendinous insertion of the Aw division of the adductor mandibulae muscle, (Fig. 1C). There is no macroscopically obvious and clearly defined connective tissue linkage between the mandible and hyoid arch in *Amblycirrhitus bimacula* (hereafter referred to as Group III).

In all three groups the adductor mandibulae Aw division originates on the quadrate through a posterior extension of the muscle's tendinous central aponeurosis, and thus is of the basic perciform type as defined by Gosline (1986). The extension is well-demarcated and moderately deep, and lies across the quadrate-anguloarticular joint. *Amblycirrhitus bimacula* (the single Group III species examined) is exceptional in this respect because the tendon lies very slightly above the jaw articulation. Members of all three groups have the fascia covering the Aw muscle extending posteriorly onto the lower half of the quadrate, part of the preoperculum, and the upper margin of the interoperculum as well.

Within the three species of Group I there are differences in the association between the mandibulohyoid connection and the tendon of the adductor mandibulae A_1 muscle inserting on the maxilla. *Cyprinocirrhites polyactis* is unique in having what appears to be a short branch of the mandibulohyoid connection arising near the latter's attachment to the coronoid process of the dentary and then joining the maxillary tendon of the adductor mandibulae A_1 muscle (Fig. 1A). In *Cirrhitichthys oxycephalus* and *Cirrhitops fasciatus*, the maxillary tendon partially fuses with the mandibulohyoid connection at the point where the two cross over each other (the latter lying medial to the maxillary tendon). From the point of fusion a short section (interpreted as a continuation of the maxillary tendon) runs into the tendinous central aponeurosis of the adductor mandibulae Aw muscle (Fig. 1B).

There are also intergroup differences in other ligamentous and tendinous linkages (Fig. 1). Species of Groups I and III have a small upper, anterior division of the adductor mandibulae muscle A_1 inserting onto the maxilla only *via* the ligamentum primordium. Group II species, in contrast, have

that division of the muscle inserting on the maxilla through both the *ligamentum primordium* and the maxillary ligament of adductor mandibulae A_1 muscle. In all three groups the major (*ie* lower) division of the muscle is attached to the *ligamentum primordium* and the maxillary ligament, the latter inserting on the ventral aspect of the maxilla, and the former on the bone's dorsolateral aspect.

Other intergroup differences involve the epihyal-interopercular and the interhyal-interopercular ligaments (For comparison of these and other ligaments with the situation in other cirrhitoid families, see pp. 94 and pp. 97–98 and Figs 2–4). Group II species have the latter ligament partly associated with the epihyal as well as the interhyal, as does the single Group III species dissected; in Group I taxa, however, the ligament is confined to the interhyal. The epihyal-interopercular ligament shows more marked intergroup differences, especially when species of Group I are compared with those of the other two groups, a difference possibly associated with the manner in which the epihyal contacts the interoperculum. In Group II taxa, the lateral face of the epihyal head articulates with a well-defined, prominently raised and posteriorly directed facet situated a little below the dorsal margin of the interoperculum and slightly behind the bone's midpoint. The epihyal-interopercular ligament in these fishes is short and stout, originates on the lateral face of the epihyal near its dorsal tip, and runs forward at approximately 45 to the sagital plane. It inserts on the upper and anterior faces of the prominence supporting the facet on the interoperculum against which the epihyal articulates. A similar epihyal-interopercular ligament occurs in the single Group III species examined, *viz. Amblycirrhitus bimacula*. However, in this species, unlike those of Group II, the interopercular facet is located on a relatively lower base.

The epihyal-interopercular ligament is most distinctive in Group II. In species of this group (unlike the other groups) the epihyal articulates directly with the medial face of the interoperculum and not with a facet carried on a distinct and elevated base (albeit only slightly so in the single Group III species examined). The ligament itself is a prominent feature originating (as in other groups) on the dorsal tip of the epihyal's lateral face, from which it runs anteriorly onto the dorsal margin of the interoperculum at a point near the bone's anterior tip, where it is narrowly separated from the attachment point of the mandibulo-interopercular ligament (*cf. Acantholatris monodactylus* Fig.3 & p. 94).

A short interhyal-metapterygoid ligament is present in all three groups.

No interhyal-preopercular ligament is present in any examined species of the three groups (*cf.* the other cirrhitoids described below).

A stout mandibulo-interopercular ligament (Fig. 1C; lig. 3) is present in taxa of the three groups. It is confined to the lateral face of both elements in all species except *Cyprinocirrhites polyactis* and *Cirrhitichthys oxycephalus* (both members of Group I). In these two species it divides anteriorly to insert on both the lateral and the medial aspects of the anguloarticular bone.

Also common to species of the three groups is a short and deep, ventrally located ligament connecting the anguloarticular and dentary.

The family Latridae

There are clear-cut differences in certain aspects of the ligamentous and other connective systems in the two latrid species examined, namely the monotypic genus *Mendosoma lineatum* (Gay) and the species *Acantholatris monodactylus* (Carmichael) of that polytypic genus. Also, an upper division of the adductor mandibulae muscle A_1 is absent in *A. monodactylus* whereas in *Mendosoma* it is an elongate, rather thin element which lies lateral to the major part of the muscle and extends over the greater part of its length. The minor division, unlike the major one, has no direct connection with the ligamentum primordium and inserts on the maxilla, together with the major division, *via* the maxillary tendon of the A_1 muscle.

In *Mendosoma* the adductor mandibulae Aw division is a very thin muscle, largely tendinous and with a single posterior extension of its tendinous aponeurosis. This runs slightly below the upper point of the articulation of the lower jaw with the quadrate, to which bone it is attached a short distance from the anterior border (Fig. 2; tendon 3). In other words, it is of the basic percomorph type *sensu* Gosline (1986), except that in *Mendosoma* it has one prolongation extending along the symplectic, another running ventrally to attach to the medial aspect of the preoperculum, a third, directed dorsally to insert on the quadrate, and a fourth directed obliquely backwards to attach to the ventral aspect of the interoperculum medially and anteriorly.

In all essentials, the adductor mandibulae Aw tendon system's extension onto the interoperculum and preoperculum in *Mendosoma* is very similar to that in *Acantholatris*, with that in *Mendosoma*, as it were, foreshadowing the more clearly differentiated condition in *Acantholatris* (*cf.* Figs 2 & 3).

There is no ligament-like connection between the mandible and hyoid arch in *Mendosoma* (*cf. Acantholatris*; Fig. 3).

The epihyal-interopercular ligament is stout and short, connecting the lateral aspect of the epihyal with the dorsal margin of the interoperculum a short distance anterior to its slightly raised facet for articulation with the epihyal. Unlike the backward-facing facet in those cirrhitids in which it occurs, that in *M. lineatum* faces forward (Fig. 2), as it does in the other latrid examined (*Acantholatris monodactylus*; and in the cheilodactylids dissected).

A discrete interhyal-interopercular ligament (present in cirrhitids) is apparently lacking in *M. lineatum* (as it is also in *Acantholatris*, and *Cheilodactylus*).

Like the two latter genera, but not in the cirrhitids examined, *Mendosoma* has a well-developed interhyal-preopercular ligament and another, more dorsally placed ligament between the interhyal and the metapterygoid (Fig. 2; lig. 7). This latter ligament I consider to be the homologue of the interhyal-quadrate ligament in *Cheilodactylus*, and the ligament in *Acantholatris* which runs from the interhyal to both the quadrate and the entopterygoid (see p. 98 & p. 99 respectively).

Mendosoma has discrete lateral and medial divisions of the mandibulo-interopercular ligament, with the medial division terminating a short distance behind the anterior tip of the interoperculum (Fig. 2; lig. 6), and the lateral division extending much further posteriorly.

The anguloarticular-dentary ligament is short and stout, markedly stouter than in any cirrhitid species examined, and stouter than that in *Acantholatris*.
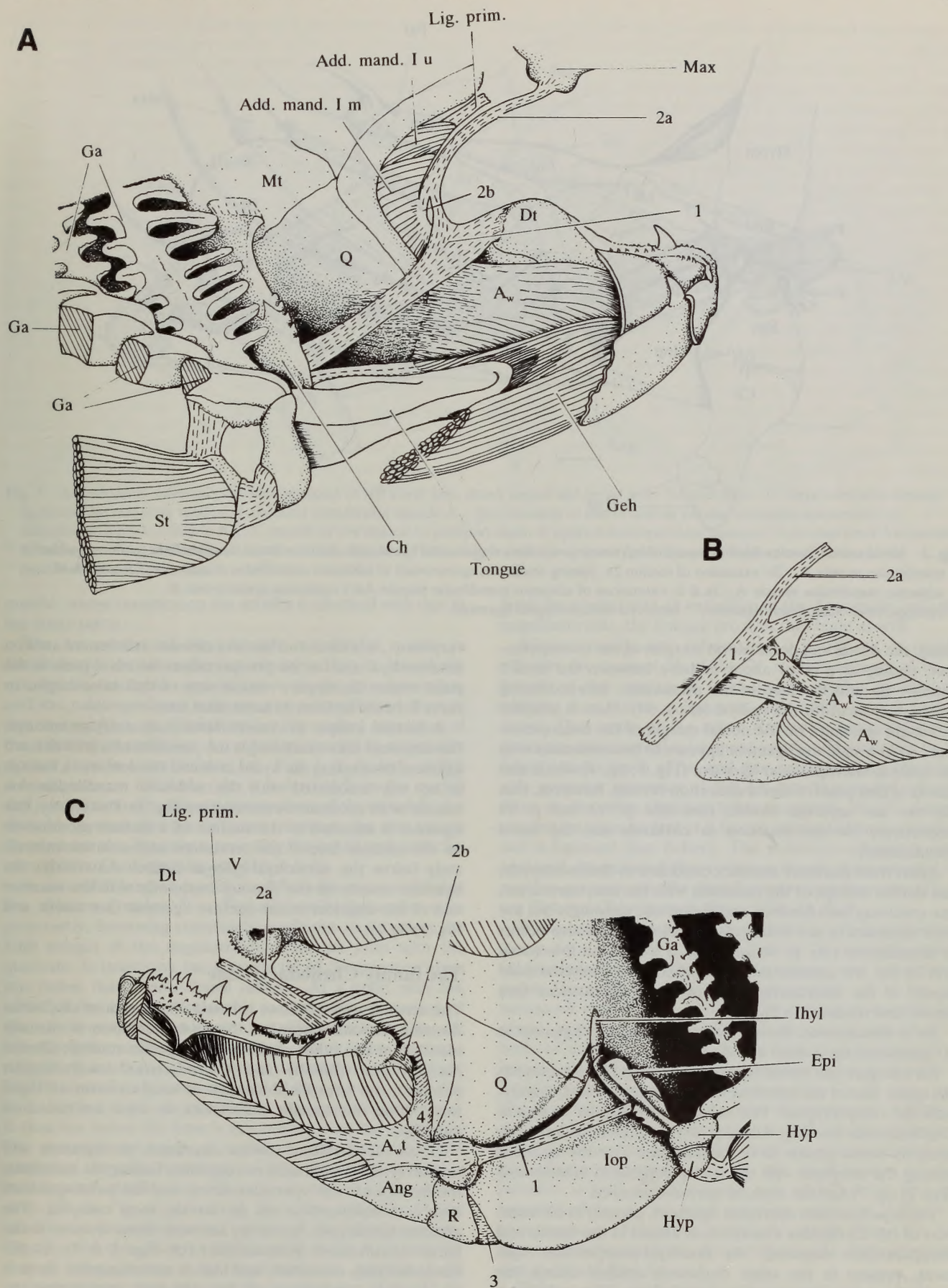
As compared with the ligamentous and other connective tissue systems in *Mendosoma lineatum*, those in *Acantholatris monodactylus* are considerably more complex, (as they are when compared with the cirrhitid species studied). As was noted earlier (p. 94), there is no obvious sub-division of the adductor mandibulae A_1 muscle in *A. monodactylus*. However, anteriorly the upper third of the muscle, unlike the other two-thirds, is free from the ligamentum primordium and inserts on the maxilla only through the maxillary tendon, to which the major part of the muscle is also attached.

Acantholatris monodactylus has a substantial Aw portion of the adductor mandibulae muscle. From the muscle's mediolateral tendinous aponeurosis a stout and relatively short branch (tendon 3 in Fig. 3) runs posteriorly to insert on the anteromedial aspect of the preoperculum's horizontal limb.
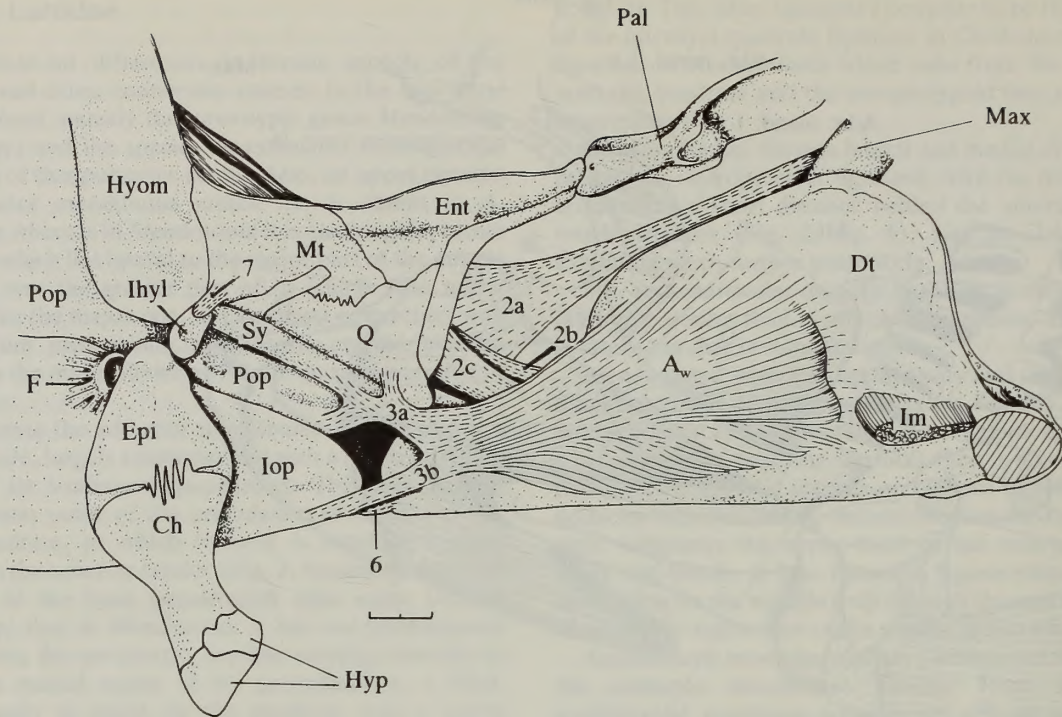
A second stout and much longer tendon from the Aw muscle (tendon 5 in Fig. 3) extends from the ventral margin of the muscle above the anguloarticular bone, and runs obliquely backwards to attach to the medial aspect of the interoperculum a short distance from that bone's anterior tip. This tendon, unlike tendon 3, is not derived from the aponeurosis of the adductor mandibulae Aw muscle but originates directly from the muscle itself. Immediately after its origin, tendon 5 is attached to the anterodorsal aspect of the anguloarticular's medial face. It then passes over that face of the retroarticular, and attaches to the medial aspect of the interoperculum a short distance from the bone's anterior tip. Since this tendon links the mandible with the interoperculum it would appear to be the functional equivalent of the mandibulo-interopercular ligament in the other species described above. However, a true and very long mandibulo-interopercular ligament is also present in *A. monodactylus* (Fig. 3; lig. 6). Anteriorly it has an extensive attachment to the lateral face of the anguloarticular and retroarticular bones, as well as another on the posterior face of the retroarticular. From here the ligament extends across to, and

Fig. 1 A: *Cyprinocirrhites polyactic* (Group I species) Medial aspect of the left lower jaw, cheek region and hyoid arch, viewed obliquely from above, to show the mandibulohyoid connection (semi-schematic). The branchial skeleton is displaced to the right. About times natural size. 1: Mandibulohyoid connection; 2a: tendon from lower part of adductor mandibulae A_1 muscle to maxilla; 2b: continuation of tendon 2a, joining tendinous aponeurosis of adductor mandibulae muscle Aw. Lig. prim: Ligamentum primordium.

B: *Cirrhitops fasciatus* (Group I species) Diagramatic representation of mandibulohyoid connection and related tendons; medial aspect of left side to demonstrate the second form of tendinous relationships within species of Group I. Abbreviations as in Fig. 1A.

C: *Paracirrhites forsteri* (Group II species). Medial aspect of the right lower jaw, cheek region and hyoid arch, viewed somewhat dorsally; the branchial skeleton and hyoid arch considerably displaced to the left and posteriorly in order to reveal the mandibulohyoid connection. (Semi-schematic). About times natural size. 1: Posterior portion of mandibulohyoid connection, inserting partly on the quadrate, and partly continuous with tendinous aponeurosis of the adductor mandibulae muscle Aw (Awt); 2b: ventral continuation of maxillary tendon of adductor mandibulae muscle A_1; 3: interopercular-mandibular ligament; 4: tendon of adductor mandibulae A_2 muscle; Lig. prim: ligamentum primordium.

A

Lig. prim.

Add. mand. I u

Add. mand. I m

Max

2a

Ga

Mt

2b

Dt

1

Q

A_w

Ga

Ga

St

Geh

Ch

Tongue

B

2a

1   2b

A_w t

A_w

C

Lig. prim.

Dt   V   2a

2b

Ga

Ihyl

Epi

A_w

Q

Hyp

4

A_w t

1

Iop

Ang

Hyp

R

3

Fig. 2 *Mendosoma lineatum* Medial aspect of left lower jaw, cheek region, and hyoid arch. Scale = 2mm. 2a: Maxillary tendon of adductor mandibulae muscle A_1; 2b: extension of tendon 2a, joining tendinous aponeurosis of adductor mandibulae muscle Aw; 2c: tendon of adductor mandibulae muscle A_2; 3a & b: extensions of adductor mandibulae muscle Aw's tendinous aponeurosis; 6: interopercular-mandibular ligament; 7: interhyal-metapterygoid ligament.

along, the dorsal and dorsolateral margins of the interoperculum, ending at a point about midway between the bone's anterior tip and the face of the prominent, forward-facing articulatory facet for the epihyal (cf pp. 94). Here it attaches to a slight eminence on the dorsal margin of the interoperculum. At first sight the ligament appears to be continuous with the epihyal-interopercular ligament (Fig. 3; lig. 4) which also inserts at that point. Careful dissection reveals, however, that the two are separate entities (see also p. 93 and p. 94 respectively for the situation in cirrhitids and the latrid *Mendosoma*).

Apart from the more complex condition in cheilodactylids, this double linkage of the mandible with the interoperculum, one involving both tendons and ligaments, seemingly has not been recorded in any other teleosts. However, it also occurs in *Mendosoma* (see p. 94 and Fig. 2) where the lowermost arm of the Aw aponeurosis is attached to the anteromedial aspect of the interoperculum, and in *Cheilodactylus* (see below, and tendon 5 in Fig. 4).

As in *Mendosoma*, the anguloarticular-dentary ligament in *A. monodactylus* is short and stout.

An elongate and broad ligament (lig. 7 in Fig. 3) connects the upper face of the interhyal with the quadrate and, mainly, with the entopterygoid. This connection is similar to that in *Cheilodactylus* (see Fig. 4, and p. 98), and, from its interconnections would appear to be homologous with the ligament joining the interhyal with the metapterygoid in *Mendosoma* (Fig. 2; lig. 7) and the cirrhitid species examined.

The interhyal-interopercular ligament, present in all members of the Cirrhitidae examined, is absent in the latrids and cheilodactylids dissected. An interhyal-preopercular ligament, present in the other cirrhitoids studied except the cirrhitids, is also developed in *Acantholatris*. Here, although

very short, it is stout and has an extensive attachment area on the interhyal and on the preoperculum, which it joins at the point where the upper, vertical arm of that bone begins to curve forward to form its horizontal arm.

A feature unique to *Acantholatris monodactylus* amongst the cirrhitoid taxa examined is the presence of a well-defined ligament connecting the hyoid arch and the dentary, a linkage in no way associated with the adductor mandibulae Aw muscle or its aponeurotic system (see Fig. 3). Posteriorly, this ligament is attached to the summit of a distinct prominence on the anterior face of the ceratohyal and situated immediately below the ceratohyal-epihyal suture. Anteriorly, the ligament inserts on the dentary conjointly with the anterior end of the anguloarticular-dentary ligament (see above and Fig. 3; lig.1).

The family Cheilodactylidae

The account which follows is based on dissections of *Cheilodactylus fasciatus* Lacepède. Since the situation is virtually identical in two other cheilodactylid species studied, *Cheilodactylus pixi* (Smith) and *Chirodactylus brachydactylus* (Cuvier), the term *Cheilodactylus* is used to cover all three taxa. What interspecific differences do exist are noted on page 98.

Of all the cirrhitoid species examined, the ligament and tendon systems separately or conjointly linking the mandible, the hyoid arch, the opercular series, and the palatoquadrate arch in *Cheilodactylus* are by far the most complex. The greatest similarities, however, are with those systems in the latrid *Acantholatris monodactylus* (cf. Figs 3 & 4). In the cheilodactylids examined, and like *A. monodactylus*, there is no obvious subdivision of the adductor mandibulae A_1
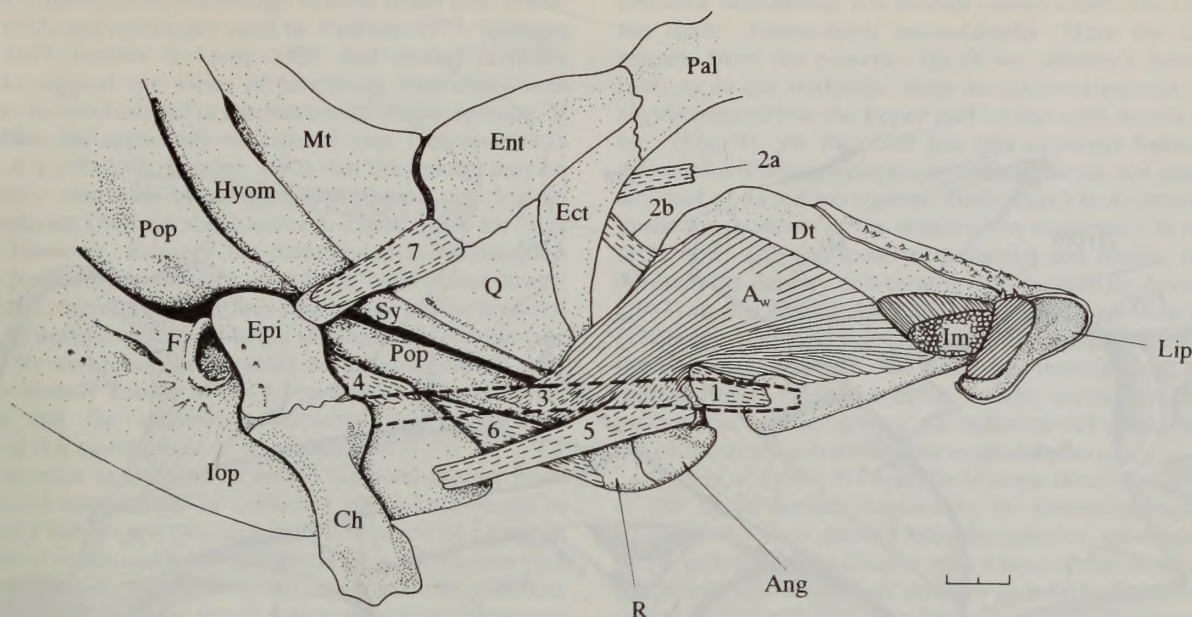
Fig. 3 *Acantholatris monodactylus* Medial aspect of left lower jaw, cheek region and hyoid arch. Scale = 2mm. 1: Anguloarticular-dentary
ligament; 2a: maxillary tendon of adductor mandibulae muscle A_1; 2b: extension of above tendon joining tendinous aponeurosis of
adductor mandibulae muscle Aw; 3: tendon of Aw muscle to preoperculum; 4: epihyal-interopercular ligament; 5: tendon from Aw muscle
to interoperculum; 6: interopercular-mandibular ligament; 7: interhyal-quadrate-entopterygoid ligament. Dashed outline that of the
mandibulohyoid connection.

muscle, whose insertion on the maxilla is identical with that in
the latter taxon.

The Aw portion of the adductor mandibulae muscle in
Cheilodactylus is noticeably less extensive than in *Acanthola-
tris*, but its tendinous connections with the interoperculum
and the palatoquadrate arch are more complicated than in
that taxon. Also, in *Cheilodactylus* the ventral extension of
the adductor mandibulae A_1 maxillary tendon is noticeably
stouter than in *Acantholatris* (cf. Figs 3 & 4) but, unlike
Acantholatris, in *Cheilodactylus* it is derived from the medial
and not the lateral tendinous aponeurosis of the muscle's Aw
division. A most obvious difference between the two taxa is
the absence of a ligament connecting the hyoid arch with the
mandible in *Cheilodactylus* (cf. Figs 3 & 4).

A somewhat tendinous section of the adductor mandibulae
Aw division (tendon 3 in Fig. 4) in *Cheilodactylus* runs
posteriorly, becoming completely tendinous as it crosses the
hind margin of the anguloarticular and its joint with the
quadrate. It inserts on the anterior tip of the preoperculum
just below that bone's dorsal margin. At a point near the
centre of the anguloarticular this partly tendinous section of
the Aw division of the adductor mandibulae muscle gives off
a ventroposteriorly directed branch which soon becomes
completely tendinous. The anterior part of this tendon (5a in
Fig. 4), immediately below its point of departure from tendon
3, is attached to the anguloarticular near its anterior margin.
It thus lies below the bone's articulation with the quadrate.
The posteriad extension of tendon 5a runs backwards and
somewhat dorsally, seemingly joining the lateral face of a
broad, stout, dense, and obliquely orientated ligament-like
strap (5b in Fig. 4) extending from the midpoint of the
quadrate to the anteroventral surface of the interoperculum.
Together the two elements (*ie* 5a and 5b in Fig. 4) form a 'Y'
shaped linkage between the anguloarticular, quadrate, and
interoperculum. Also, because the anterior arm of the 'Y' (*ie*

5a) is associated with an extension of the Aw muscle onto the
anguloarticular, the linkage involves that bone as well.

Without ontogenetic information it is difficult to decide
whether the element 5b of the 'Y' is, at it appears to be, a
branch of the tendon 5a (and thus is itself a tendon) or
whether it is strictly a ligament with which tendon 5a has
fused. That none of the other cirrhitoids examined has a
quadrato-interopercular ligament would add credence to 5b
being a true branch of 5a, and thus representing a consider-
able posterior extension of the Aw muscle's tendon system.
Also, in the other cheilodactylids examined, the 'Y'-shaped
connection gives no hint of it having originated from a tendon
and a ligament (see below). The potential complexity and
posterior extension of that system is clearly demonstrated in
another percomorph, the percid *Gymnocephalus cernua* (L.);
see Elshoud-Oldenhave & Osse (1976; fig. 4.1).

When comparisons are made with the latrid *Acantholatris*,
(see p. 94 and Fig. 3) it appears that the 'Y'-shaped complex
in *Cheilodactylus* is, from its disposition and attachment
points, homologous with the simple tendon (5 in Fig. 3)
associated with the Aw portion of the adductor mandibulae
muscle in *Acantholatris*. Tendon 5 in that taxon is attached to
both the anguloarticular and the medial face of the interoper-
culum, and is separated by a short section of Aw from tendon
3 which inserts on the preoperculum (Fig. 3). In turn, and
also from its disposition and points of attachment, the latter
tendon would seem to be homologous with the longer tendon
3 in *Cheilodactylus* which also inserts on the preoperculum.
An early evolutionary stage in the development of this
complex in both *Cheilodactylus* and *Acantholatris* may be
represented by the tripartite posterior extension of the Aw
aponeurosis in *Mendosoma*, which also serves to link the Aw
muscle with the quadrate, preoperculum and interoperculum
(see p. 94 and Fig. 2).

The two other cheilodactylid species dissected, *Chirodacty-*
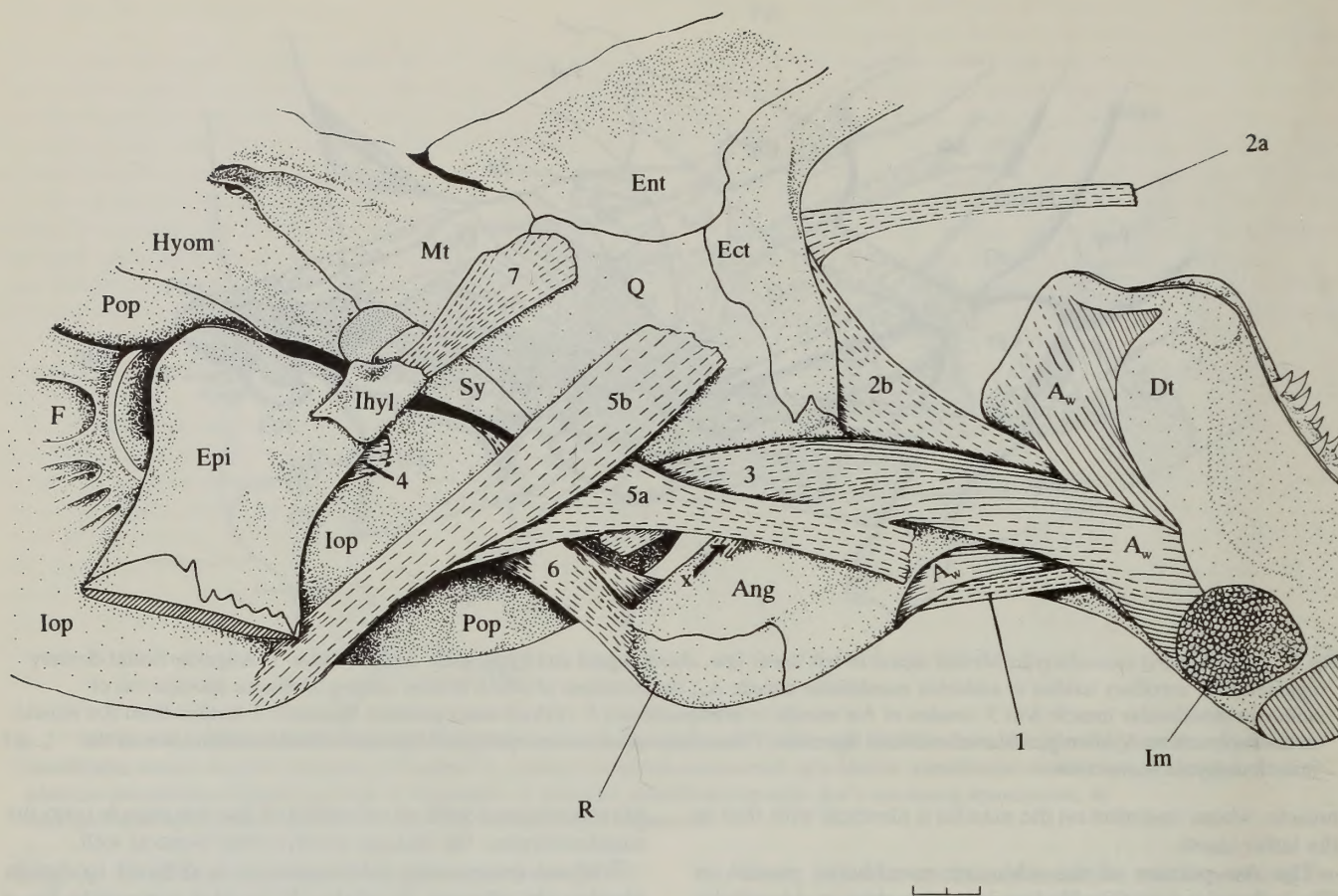
Fig. 4 *Cheilodactylus fasciatus* Medial aspect of left lower jaw, cheek region and hyoid arch. Scale = 2mm. 1: Anguloarticular-dentary ligament; 2a: maxillary tendon of adductormandibulae muscle A_1; 2b: extension of above tendon joining tendinous aponeurosis of adductor mandibulae muscle Aw; 3: tendon of adductor mandibulae muscle Aw to preoperculum; 4: epihyal-interopercular ligament; 5a: extension of tendon 3; 5b: branch of tendon 5a, attaching to quadrate above and interoperculum below; 6: interopercular-mandibular ligament; 7: interhyal-quadrate ligament; x: anguloarticular-quadrate ligament.

lus brachydactylus and *Cheilodactylus pixi*, have a mandibular-preopercular-quadrate tendon system essentially like that described above in *Cheilodactylus fasciatus*. In these species the interopercular-quadrate branch (Fig. 4; 5b) does not partly overlap that section of the complex (Fig. 4; 5a) going to the anguloarticular. Instead, the two branches meet in the same plane, with the result that the complex is clearly single and 'Y'-shaped. Since the specimens of *Chirodactylus brachydactylus* (standard length 106 mm) and *Cheilodactylus pixi* (S.L. 70–81 mm) are much smaller than the specimen of *Cheilodactylus fasciatus* (S.L. 243 mm), the difference could be related either to the larger size of the *C. fasciatus* specimen or to individual variation.

The epihyal-interopercular ligament in *Cheilodactylus* is short and broad (shorter even than that in the latrid *Mendosoma*; and unlike the long and anteriorly directed ligament in the other latrid examined, *Acantholatris,* Fig. 4; lig. 4). As in *Acantholatris*, but unlike *Mendosoma*, the interopercular facet for the epihyal in *Cheilodactylus* is prominent and well-developed (see Fig. 4). The interhyal-quadrate ligament is long and flat (Fig. 4; lig. 7), again like that in *Acantholatris*, but unlike its presumed homologue, the short and stout interhyal-metapterygoid ligament in *Mendosoma*.

The interhyal-preopercular ligament in *Cheilodactylus* is also short and stout. No discrete interhyal-interopercular

ligament is developed in the cheilodactylids, a characteristic shared with the two latrid genera examined, but not with the cirrhitid species studied.

A stout anguloarticular-dentary ligament is present, as it is in the other cirrhitoids, but unlike those taxa *Cheilodactylus* has a short and broad ligament (x in Fig. 4) connecting the uppermost part of the anguloarticular's posteromedial face to the quadrate, where it is attached to the ventral rim of that bone's facet for articulation with the anguloarticular. This small ligament, not found in any of the other cirrhitoids examined, is almost entirely hidden by tendon 5a of the 'Y' shaped complex described above.

A very stout interopercular-mandibular ligament originates laterally on the dorsal margin of the interoperculum near its anterior tip, and inserts mostly on the lateral aspect of the anguloarticular and retroarticular bones, but with a short medial branch going to the posteromedial face of the retroarticular (6 in Fig. 4).

DISCUSSION AND CONCLUSIONS

The taxonomically and phylogenetically widespread occur-

rence of a mandibulohyoid linkage in bony fishes (see Tchernavin, 1953, and references cited by Verraes, 1977, Springer *et al.*, 1877, Lauder & Liem, 1980, and above) certainly seems to support the views of functional anatomists with regard to its involvement in the mechanics of jaw opening. It also refutes the apparently widespread view (see reviews in Lauder & Liem, 1980; Lauder, 1982) that the linkage may be a primitive character of neopterygian fishes, one lost in higher teleosts (but see also Lauder & Liem, 1989, for later views). However, although the mandibulohyoid connection may be functionally homologous in both 'higher' and 'lower' bony fishes, there are indications that it may not be homologous in an ontogenetical and hence phylogenetic context (see below). Nevertheless, the diversity of mandibulohyoid connections already known in but a few teleost fishes strongly suggests that the structural, functional and ontogenetic aspects of this system need to be reevaluated.

Any attempt to establish or refute the homology of mandibulohyoid connections in cirrhitoid fishes with those in other bony fish groups (see below) is hampered by a lack of information on the ontogeny of the linkage in the various taxa involved. Indeed, this problem also arises with the different mandibulohyoid linkages found within the cirrhitoids themselves, namely those in the Cirrhitidae (p. 93) and that in the latrid *Acantholatris monodactylus* (p. 97).

The cirrhitid linkage type in the *Paracirrhites* species examined (p. 93) strongly suggests that the connection between the mandible and the ceratohyal in these fishes is derived from an extension of the central aponeurosis of the adductor mandibulae muscle's Aw portion onto the hyoid arch (with, in addition, a partial insertion on the quadrate; Fig. 1C and p. 93). In another cirrhitid group (*viz. Cyprinocirrhites polyactis*, *Cirrhitichthys oxycephalus* and *Cirrhitops fasciatus*) the connection also has a linkage with the aponeurosis of adductor mandibulae Aw. Here it is effected, somewhat indirectly, by a branch from the major mandibulohyoid connection joining the maxillary tendon of adductor mandibulae A_1 muscle, which tendon itself is derived from the aponeurosis of the Aw portion of that muscle. This association with the Aw aponeurosis in both cirrhitid groups raises the possibility that ontogenetically, the mandibulohyoid linkage is through a tendon and not a ligament as it appears to be in the salmonid *Oncorhynchus mykiss* (see Verraes, 1977). It also raises the question whether or not the so-called mandibulohyoid ligament (see below) in other teleosts (and in the semionotiform Lepisosteidae; see below) is truly a ligament. A similar problem arises with the third type of mandibulohyoid connection found in cirrhitoids, namely that in the latrid *Acantholatris monodactylus*. Here the linkage is not associated with the Aw muscle, and has both its origin and its insertion entirely on bone, thus appearing to be a true ligament.

There is some indirect support for the idea that in members of the Cirrhitidae the mandibulohyoid connection could be derived ontogenetically from the adductor mandibulae muscle bloc (*sensu* Edgeworth, 1935) of the early embryo. This stems from the considerable posterior extension of the adductor mandibulae Aw aponeurosis onto the bones of both the palatoquadrate arch and the interoperculum in certain other perciform fishes (see also discussions in Winterbottom, 1974; Elshoud-Oldenhave & Osse, 1976; Anker, 1978; Greenwood, 1985) and, indeed in other cirrhitoids such as the cheilodactylids.

An origin of the mandibulohyoid connection from the adductor mandibulae Aw tendon system seems less likely in the latrid *Acantholatris monodactylus*. Here the linkage extends from the posterior tip of the dentary's lower arm (not, as in the cirrhitids, from its coronoid process or the anguloarticular) to the upper part of the ceratohyal's lateral face (Fig. 3). At no point has this apparent ligament in *Acantholatris* any association with the adductor Aw muscle or any part of its tendon system. With regard to its attachment to the lower aspect of the dentary, the connection is comparable both with the loosely compacted and fibrous linkage between the dentary and ceratohyal identified by Aerts *et al.* (1987) in the cichlid *Astatotilapia elegans*, and with Osse's (1969) ligament XXIV in the percid *Perca fluviatilis*. In both these species, however, the tissue has insertions on certain branchiostegal rays as well as on the ceratohyal, and in neither species does it have the ligament-like appearance of the connection in *Acantholatris monodactylus*.

Aerts *et al.* (1987:97) describe in some detail the histology of the hyoid-dentary connection in *Astatotilapia elegans*, which seemingly is derived from the anterior, tendinous part of the geniohyoideus muscle, with whose dorsolateral aspect it is closely associated over much of its length. These authors conclude (*op. cit.*: 99) that 'In fact, the rostral part of the interconnection can be interpreted as a parallel elastic component of the protractor hyoidei' (=geniohyoideus). The posterior attachment of the connection is on the epi- and ceratohyals dorsally, with, as noted above, a number of small strands merging into the dermal layers of the skin-fold between the hyoid and interoperculum. A mandibulohyoid connection, superficially like that in *A. elegans* also occurs (pers.obs.) in another haplochromine cichlid, *Thoracochromis buysi* (Penrith); although its histology was not studied, the linkage appears to originate from within the geniohyoid muscle, and to attach to the hyoid arch at the epi-ceratohyal suture.

At least with regard to its superficial features, Aerts *et al.*'s description of the dentary-hyoid connection in *Astatotilapia elegans* does not resemble the condition seen in *Acantholatris monodactylus*. Here, the interconnecting tissue is clearly separated from the geniohyoideus muscle over virtually its entire length, and is much more compact and ligament-like. However, posteriorly it does appear to fuse with the tendinous insertion of the geniohyoideus at the point where both elements attach to an elevation on the anterior margin of the certohyal. The insertion of the geniohyoideus muscle then extends down along the lateral face of the ceratohyal, but that of the mandibulohyoid connection does not. Thus in adult *Acantholatris monodactylus* the only suggestion of the connection being derived from the geniohyoideus muscle is a partially shared insertion with that muscle on the ceratohyal. That suggestion is, unquestionably, far less convincing than the evidence provided by the situation in *Astatotilapia elegans*, but is one that could be clarified if studied ontogenetically in *Acantholatris monodactylus*.

A distinct mandibulohyoid ligament, superficially like that in *Acantholatris monodactylus*, has been described by Wiley (1976) in the semionotiform gars *Lepisosteus* and *Atractosteus*. The connection is labeled as a tendon in figure 9 of Wiley's paper, but is referred to, I believe correctly, as a ligament in the accompanying text. The ligament in gars differs from the ligament-like mandibulohyoid connection in *Acantholatris monodactylus* in its points of attachment (epihyal and retroarticular in the gars, ceratohyal and dentary in *A. monodactylus*). Again, without ontogenetic information

from both taxa, nothing can be said about its possible homology in the two species.

The concept that a mandibulohyoid connection (usually referred to as a ligament) is essentially a feature of pre- and lower teleost actinopterygians, has influenced theories relating to the evolution of feeding machanisms in teleosts. For example, Lauder (1982: 279, also fig. 1) postulated that 'The first specialization involves a shift of insertion of the mandibulohyoid ligament to the interoperculum. The interoperculohyoid ligament characterizes the feeding mechanism of eurypterygian fishes (=Aulopiformes + Myctophiformes + Paracanthopterygii + Acanthopterygii; Rosen, 1973) and effectively shifts the action of the hyoid and opercular coupling onto the interoperculum. Only the interoperculomandibular ligament transmits posterodorsal hyoid and opercular movements to the mandible in the Eurypterygii, while other teleosts retain the primitive two-coupling system of the halecostomes' (ie both a mandibulohyoid and an interopercular-mandibular linkage). Verraes' (1977) studies on the development of Oncorhynchus mykiss show unequivocally that in this teleost there is no ontogenetic shift of the mandibulohyoid ligament's mandibular insertion onto the interoperculum. Indeed, the interopercular-mandibular ligament develops independently (and later than the mandibulohyoid ligament) with both connections persisting in adults (Verraes, 1977; pers. obs.); neither is there any ontogenetic evidence to show that the epi- (or inter-) hyal to interoperculum ligament is the result of a preexisting mandibulohyoid ligament shifting its mandibular insertion onto the interoperculum. Interestingly in that context, the latrid Acantholatris, which has what appears to be a genuine mandibulohyoid ligament (see p. 97) also has an epihyal-interopercular ligament.

Thus, pace Lauder (1982), it would seem that cirrhitoids (and other teleosts) with both a mandibulohyoid connection and an interopercular-mandibular ligament have either retained the primitive halecostome condition or, as seems more likely, re-evolved it through some other form of connective tissue linkage between the hyoid arch and the mandible.

Parenthetically, it may be noted that the importance of an interopercular-mandibular linkage in the jaw-opening mechanism of teleosts, stressed by Lauder op.cit. and other authors (see for example Liem, 1978 & 1991; Aerts et al., 1987, and references therein) is underlined, albeit indirectly, by the condition in three of the cirrhitoid taxa examined. In Cheilodactylus (Cheilodactylidae) and in Mendosoma and Acantholatris (Latridae) there is, in addition to the interopercular-mandibular ligament a second such linkage effected through an extension of the Aw muscle's aponeurotic system onto the interoperculum (see pp. 94 & 97 and Figs 2–4).

If, as suggested above, certain teleosts have re-evolved a mandibulohyoid connection, it may have arisen in different ways. This seems probable even within the cirrhitoids (viz. cirrhitid and latrid types; see pp. 93 & 94), and in other groups as well. In the ostariophysan Hydrocynus vittatus (Characidae) for example, the mandibulohyoid connection appears to be an extension of the epihyal-interopercular ligament which, after its insertion on the dorsal margin of the interoperculum, continues forward to bridge the small gap between that bone and the retroarticular (pers. obs.). The salmonid Oncorhynchus mykiss, by contrast, has no obvious association of the mandibulohyoid connection with the epihyal-interopercular ligament. Both are discrete entities

throughout their lengths despite having insertion points close together on the epihyal (pers. obs.). The clupeid Etrumeus, unlike the preceding examples, has no readily discernible mandibulohyoid connection. However, the geniohyoideus muscle has a thickened and tendinous dorsal margin which is macroscopically continuous with the muscle from the latter's origin near the dentary symphysis to its insertion immediately over the epi-ceratohyal suture (pers. obs). Superficially at least, the situation in this clupeid shares certain similarities with the mandibulohyoid link in the perciform cichlid Astatotilapia elegans (see Aerts et al., 1987, and p. 99 above). In the clupeid, however, the differention of the linkage from the associated muscle is at a somewhat lower level of development than that in the cichlid.

Verraes (1977) highlighted the functional importance of the mandibulohyoid connection in immediately post-hatching stages of the salmonid Oncorhynchus mykiss. This apparently ligamentous connection develops earlier than the interopercular-mandibular ligament. Thus at this point in the fish's life-history it is an essential element in bringing about jaw depression, and consequently it plays a major role in the creation of the trans-buccal water current involved in respiration and feeding (see also Lauder & Liem [1989] for a discussion of this ligament in the feeding mechanism of another salmonid, Salvelinus fontinalis). Recently, Aerts et al., (1987), working with the cichlid Astatotilapia elegans, postulated that a mandibulohyoid connection is also of crucial importance in the feeding mechanism in adults of that species.

Regretably, no experiental work has been carried out on the feeding mechanisms of cirrhitoid fishes, nor is there enough critical information on their feeding habits to determine what correlations may or may not exist between species with or without a mandibulohyoid connection. It would be interesting to know in what way the mandibulohyoid connection functions in cirrhitids such as Cyprinocirrhites polyactis. Judging from preserved specimens it would seems to block the sinking of the lower jaw when the hyoid is pulled posteriorly by the contracting sternohyoideus muscle – a somewhat anomalous situation, but possibly one that may be associated with a specialized suction mode of feeding on small crustacean zooplankters, apparently the principal food of this species in South African waters.

As yet, the intrabuccal tendon and ligament systems are known from too few cirrhitoid taxa to test its usefulness in the intragroup taxonomy and phyletic relationships of those fishes. However, the tendon system in the Cheilodactylidae examined, when compared with that in the latrid Acantholatris monodactylus (cf. Figs 4 & 3) supports the latter taxon's removal (see Greenwood, 1995) from the genus Cheilodactylus and the family Cheilodactylidae in which it had been placed previously. Those differences also provide an additional character complex for distinguishing the Latridae from the Cheilodactylidae.

untidy manuscript into a legible typescript. Anthea Ribbink, who also displayed those attributes when producing the anatomical figures, deserves my deepest gratitude for her essential contributions to this paper. By no means least of all, I am indebted to Drs Mark Westneat and Rick Winterbottom for their very constructive comments on an earlier draft of the paper.

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A new species of *Crocidura* (Insectivora: Soricidae) recovered from owl pellets in Thailand

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SYNOPSIS. A new species of *Crocidura* (white-toothed shrew) is described from owl pellets from Loei Province, Thailand. The craniodental morphology is compared with that of similar sized species of *Crocidura* recorded from Thailand.

INTRODUCTION

A recent survey of bat roosts and owl pellets in Thailand by one of us (ALS) and Mark F Robinson has increased knowledge of the small mammal fauna of the area. Contained in the owl pellets were skulls of 38 species of small mammals, including an unknown species of *Crocidura*. This undescribed species has sufficiently distinctive cranial and dental characters to warrant its description on the basis of these features alone, although the external characters remain unknown.

MATERIALS AND METHODS

Regurgitated pellets were collected from roosting sites of barn owls (*Tyto alba* [Scopoli, 1769]) at several localities in Thailand. The pellets were dissected and the contents, usually incomplete crania and mandibles, were identified as far as possible in the field. Voucher specimens were sent to The Natural History Museum for confirmation of identification. Included among these specimens was a series of *Crocidura* which was proving difficult to identify and was thought to include two species, *C. attenuata* Milne-Edwards, 1872 and *C. fuliginosa* (Blyth, 1855).

Measurements, in millimetres, were taken using dial calipers or a micrometer eyepiece and measuring stage on a microscope. Cranial and dental nomenclature follows that of Meester (1963), Mills (1966), Swindler (1976) and Butler & Greenwood (1979). Abbreviations for the dental nomenclature are given in the text.

RESULTS

Crocidura hilliana sp. nov.

HOLOTYPE. BM(NH)1994.90, collector's number 467. Cranium with damaged braincase, left mandibular ramus, com-

plete maxillary and mandibular dentition. Extracted from an owl pellet from a roost at Wat Tham Maho Lan, Ban Nong Hin, 48 km south of Loei, Loei Province, northeastern Thailand, 17°06′N 101°53′E, altitude 575m.

PARATYPES. Eighteen specimens of crania with mandibles and thirteen specimens of crania only, all from owl pellets at the same locality as the holotype. Three specimens of crania with mandibles and five specimens of crania only from Wat Tham Pha Phu, 7 km north of Loei, Loei Province, 17°34′N 101°42′E, altitude 542m.

Diagnosis

Zygomatic process of maxilla broad and angular, interorbital region narrow; coronoid process broad and deep. Upper and lower first incisors robust, first upper unicuspid large and broad relative to the other unicuspids, talonid of the third lower molar (M_3) reduced to a single cusp.

Description

Overlapping in cranial size with medium to large specimens of *Crocidura attenuata* and smaller specimens of *C. fuliginosa* but differing from both species in proportions (see Table 1 and Figs 1–6). Cranium and mandible robust; cranium angular in appearance, especially in dorsal view. The rostrum is moderately deep and obliquely sloping anteriorly; the maxillary region is broad, the zygomatic process of the maxilla is broad and angular; the interorbital region is long and narrow, its width increasing only slightly from anterior to posterior; the zygomatic plate is positioned above the first upper molar (M^1) and the anterior of the second upper molar (M^2), its posterior face is semi-circular and deeper than the anterior face; the braincase is angular, with pronounced angular superior articular facets in dorsal view, a squamosal crest is present and lambdoid crests are well developed, meeting at an acute angle at the midline. The horizontal ramus of the mandible is moderately robust; the coronoid process is broad and deep (see Fig. 4); the ascending ramus is long and low; the condyle is nearly as broad or broader than deep (ratio of

Fig. 1 Dorsal view of cranium from left to right of *C. attenuata* BM(NH)1911.9.8.26, *C. hilliana* BM(NH)1994.113 and *C. fuliginosa* BM(NH)1933.4.1.183.

condyle width to height 91.2–113.3), the postero-internal ramal fossa has a broad base and is approximately as broad as deep; the mental foramen is positioned below the anterior part of the first lower molar (M_1).

The dentition is illustrated in Figs 2–6. The first upper incisor (I^1) is robust, slightly proodont with well developed posterolingual and posterobuccal cingula; the upper unicuspids are overlapping and crowded; the first upper unicuspid (Un^1) is large and broad in comparison with the other unicuspids, its breadth is equal to or greater than the distance between the two first unicuspids and this tooth is more than two thirds the height of I^1 and P^4; the second and third unicuspids (Un^2 and Un^3) are subequal in size; the upper premolar (P^4) has a moderately small parastyle and robust metacone; the first and second upper molars (M^1 and M^2) show no significant distinguishing features; the third upper molar (M^3) is short and slender with a slightly compressed lingual basin. The first lower incisor (I_1) is robust, long, deep and curved, and the anterolingual ridge extends for *circa* three quarters of the length of the tooth, diverging from the ventral border, the posterior border of I_1 lies below the middle of the lower premolar (P_4); two thirds of the second lower incisor (I_2) are in contact with I_1 and one third of the tooth is overlapped by P_4; the postentoconid ledge is very narrow in the first lower molar (M_1) and yet more reduced in the second lower molar (M_2); the talonid of the third lower

molar (M_3) is reduced to a single cusp.

Etymology

This species is named in honour of John Edwards Hill, who taught one of the authors (PDJ) the basics of mammalogy and who also provided invaluable help in the identification of some of the skull fragments of bats found during the survey.

Comparison with other species

Five species of *Crocidura* have been recorded from Thailand (Lekagul & McNeely, 1977, Davison, 1984): *C. fuliginosa* (including *C. dracula* Thomas, 1912 listed as a separate species by Lekagul and McNeely), *C. attenuata*, *C. pullata vorax* Allen, 1923 (listed as *C. russula vorax*), *C. horsfieldii indochinensis* Robinson & Kloss, 1922 and *C. monticola* Peters, 1870. *Crocidura hilliana* is separated from most specimens of *C. fuliginosa dracula* by its smaller size (see Table 1), while it is considerably larger than *C. p. vorax* (condylobasal length <17.5), *C. horsfieldii* (condyloincisive length <17.9, data taken from Heaney & Timm (1983) for specimens from Vietnam) or *C. monticola* (condylobasal length <17.4).

Crocidura hilliana falls at the middle to upper part of the cranial size range of *C. attenuata* and the lower part of the size

Fig. 2 Ventral view of cranium from left to right of *C. attenuata* BM(NH)1911.9.8.26, *C. hilliana* BM(NH)1994.113 and *C. fuliginosa* BM(NH)1933.4.1.183.

range of *C. fuliginosa* (see Table 1). It is readily distinguished from both species by its robust, angular cranium, in which the maxillary region is broad, the interorbital region narrow and the anterior part of the braincase markedly angular (see Figs 1–3). In contrast, both *C. attenuata* and *C. fuliginosa* have a proportionally narrower maxillary region, broader interorbital region increasing noticeably from anterior to posterior and a more rounded braincase that is evidently broader than the maxillary region. Lambdoid crests are more or less well developed in both *C. hilliana* and *C. fuliginosa*, but they meet at an acute angle at the midline in *C. hilliana* and a shallower angle in *C. fuliginosa*; lambdoid crests are less developed in *C. attenuata* and meet at a shallow angle. Squamosal crests are absent or ill defined in *C. attenuata*, poorly to moderately defined in *C. fuliginosa* but well-marked in *C. hilliana*. The mandible of *C. hilliana* is considerably more robust than that of either of the other two species (see Fig. 4). The horizontal ramus of the mandible of *C. attenuata* is more slender than that of *C. hilliana*, with a sinuous ventral border; the coronoid process is considerably narrower and shallower; the ascending ramus is higher and the condyle is higher than broad (ratio of condyle width to height 75.0–93.3). The horizontal ramus of the mandible of *C. fuliginosa* is longer yet shallower than that of *C. hilliana*, with a narrower, less robust coronoid process and, as in *C. attenuata* the condyle is higher than broad (ratio of condyle width to height 77.8–93.3). The

mental foramen lies below the posterior part of P_4 in *C. attenuata* and *C. fuliginosa* but below the anterior of M_1 in *C. hilliana*. Dentally the most obvious differences between *C. hilliana* and the other two species is the comparatively large anterior dentition (I^1, Un^1 and I_1) relative to the rest of the teeth, in combination with the narrow M^3 and the reduced M_3 of *C. hilliana*, differing considerably from the condition in either *C. attenuata* or *C. fuliginosa* (see Table 1 and Figs 2–6).

In detail the dentition of *C. attenuata* differs in the following aspects from that of *C. hilliana*: I^1 is slender and orthodont, the posterolingual cingulum is narrow, Un^1 is moderate in size and the distance between the two first upper unicuspids is greater than the breadth of Un^1, Un^2 is smaller than Un^1 and Un^3, and the unicuspids overlap only slightly so that the rostrum is moderately long in appearance; the parastyle of P^4 is moderately well developed. M^3 is variable in different populations of *C. attenuata*; it is medium sized in Indian and Burmese populations and thus readily distinguished from *C. hilliana*, and although only narrower on average in the Chinese populations of *C. attenuata*, nevertheless, the lingual basin is less compressed than in *C. hilliana*. The first lower incisor of *C. attenuata* is moderately slender, straighter and more procumbent than that of *C. hilliana*; the anterolingual ridge extends for two thirds the length of the tooth and is subparallel to the ventral border of the tooth; the posterior border of I_1 lies below the posterior part of I_2; less

Table 1 A comparison of species of *Crocidura* occuring in Thailand and nearby countries.

	C. hilliana Thailand	*C. attenuata* China	India	*C. fuliginosa* Thailand	Vietnam	China
Condylobasal length	21.0–23.5	19.8–20.7	19.7–21.6	22.0, 22.8	21.3–23.4	21.6–22.7
mean	22.20	20.20	20.23		22.58	22.20
SD	0.68	0.38	0.54		0.51	0.47
n	16	8	10	2	15	4
Upper toothrow length	8.8–10.2	8.7–9.4	8.7–9.8	10.1–10.8	9.8–10.8	9.7–10.7
mean	9.45	9.00	9.12	10.42	10.25	10.17
SD	0.35	0.23	0.29	0.29	0.27	0.35
n	37	12	17	5	24	11
Maxillary breadth at level of M^2	6.0–7.2	5.7–6.4	5.8–6.5	6.6–7.0	6.7–7.3	6.7–7.2
mean	6.57	6.14	6.08	6.72	6.96	6.91
SD	0.30	0.21	0.19	0.16	0.15	0.17
n	38	12	17	5	23	11
Interorbital breadth	3.8–4.6	4.2–4.8	4.2–4.7	4.4–4.7	4.7–5.3	4.7–5.2
mean	4.27	4.46	4.39	4.55	4.93	4.93
SD	0.21	0.19	0.12	0.13	0.13	0.19
n	38	10	15	4	22	8
Braincase breadth	8.9–10.0	8.5–9.5	8.7–9.8	9.9–10.1	9.8–10.7	9.9–10.6
mean	9.56	9.09	9.08	10.00	10.24	10.14
SD	0.36	0.34	0.33	0.12	0.24	0.26
n	16	9	11	3	18	5
Mandible length excluding I_1	10.7–12.7	10.0–11.5	10.1–11.2	11.8–12.4	11.7–13.1	11.5–12.7
mean	11.35	10.71	10.62	12.09	12.36	12.06
SD	0.55	0.46	0.42	0.24	0.35	0.41
n	21	13	17	8	26	11
Mandible height	5.2–6.3	4.4–5.1	4.5–5.2	5.2–5.8	5.4–5.9	5.2–6.0
mean	5.78	4.81	4.65	5.54	5.61	5.62
SD	0.28	0.22	0.21	0.18	0.16	0.25
n	21	13	17	9	26	9
Interorbital breadth: maxillary breadth	60.5–70.5	68.8–77.7	68.3–77.6	65.7–69.7	67.1–75.4	68.9–73.2
mean	65.00	72.36	72.40	67.43	70.86	71.09
SD	2.44	2.98	2.48	1.66	2.26	1.55
n	38	10	15	4	22	8
Length of M^3: upper toothrow length	5.2–7.0	6.4–6.9	7.1–8.0	6.8–7.9	6.6–8.0	6.9–8.0
mean	6.12	6.67	7.50	7.48	7.28	7.34
SD	0.51	0.16	0.28	0.42	0.42	0.35
n	34	12	17	5	24	10

than half of I_2 is in contact with I_1 and I_2 is one quarter overlapped by P_4; a postentoconid ledge is present in M_1 and M_2; the talonid of M_3 is relatively complete and an entoconid, entoconid ridge and talonid basin are present.

Crocidura fuliginosa differs from *C. hilliana* in having a moderately slender, orth-opisthodont I^1 with a smaller although well developed posterolingual cingulum; Un^1 is moderate in size (c half the height of I^1 and P^4); in contrast to the condition in *C. attenuata*, Un^2 is only slightly smaller than Un^1 and Un^3; the lingual region of P^4 is characteristic in shape; the mesostyle of M^2 is divided into two stylar cusps (see Ruedi, in press) unlike either of the other species; M^3 is medium in size and the lingual basin is not compressed. The mandibular dentition is similar to that of *C. attenuata*. In particular it is readily distinguished from *C. hilliana* by the less robust, straighter, more procumbent first lower incisor; slightly over half of I_2 is in contact with I_1; the talonid of M_3 is not reduced and an entoconid, entoconid ridge and talonid basin are present.

DISCUSSION

It is known from the study of barn owl pellets in the British Isles and Africa (Glue, 1967; Andrews 1990) that prey skeletal elements are subject to little breakage or digestion, contrary to the case for pellets of some other avian predators. Certainly there is a degree of damage to all of the crania in the current sample, none of which are intact. Crania and associated mandibles occur in 48%; a few specimens are nearly complete showing only minimal damage to the braincase, although the braincase is broken or absent in most specimens. The toothrows are complete in 87% of specimens, although the teeth may be loose in their sockets, with tooth loss occuring generally at the terminal molar or unicuspid loci. There is little evidence of digestive erosion of crania or teeth. It has therefore proved possible to take most of the standard cranial measurements on sufficient of the recovered crania and mandibles to obtain significant data on size variation. Similarly, the dentition is well preserved so that diagnostic characters are readily observed and allowing the samples to be aged. Shrews of the genus *Crocidura* show very rapid dental maturation as nestlings, teeth are fully erupted shortly after leaving the nest. The dental ages appearing in these samples include fully erupted dentitions with no sign of tooth wear, probably representing juvenile or subadult specimens; dentitions showing slight to moderate wear, representing adults; dentitions showing extreme wear, representing old adults.

Fig. 3 Lateral view of cranium from top of *C. attenuata* BM(NH)1911.9.8.26, *C. hilliana* BM(NH)1994.113 and *C. fuliginosa* BM(NH)1933.4.1.183.

There have been few systematic collections of the small mammal fauna in Thailand, which in consequence remains comparatively little known; in particular the shrews are poorly documented. *Crocidura fuliginosa* was recorded from peninsular Thailand by Bonhote (1903), Kloss (1917) [as *C. aagaardii*], Robinson & Kloss (1923) and Hill (1960) [probably referring to the same specimen as Robinson & Kloss (1923)], and from Koh Samui off the east coast of peninsular Thailand by Robinson & Kloss (1914) [as *C. negligens*]. The inclusion in this taxon of two chromosomally distinct but morphologically cryptic species in Malaysia was discovered recently by Ruedi *et al.* (1990). Ruedi (in press) has attempted to correlate morphological features with these chromosomal forms, in order to assign specific names to them, reserving the name *C. fuliginosa* for those specimens with chromosomes 2n = 40, Fundamental Number 56 and ascribing the other species, with polymorphic chromosomes of 2n = 38–40, to *C. malayana* Robinson & Kloss, 1911. Regrettably, examination of Malaysian specimens in the collection of the Natural History Museum fails to confirm the supposedly clearcut morphological distinction, with some specimens exhibiting a mixture of the characters listed by Ruedi, so negating the use of these morphological criteria. *Crocidura fuliginosa* is a widely distributed species, occuring from Burma in the west to China in the east and southwards to Indonesia, including a number of named forms, whose

taxonomic status has been the subject of considerable discussion (Medway, 1965, 1977; Jenkins, 1976, 1982; Heaney & Timm, 1983; Corbet & Hill, 1992). The presence of cryptic species in Malaysia, emphasises the lack of understanding of the status of *C. fuliginosa*, suggesting that it requires further revision and might be more appropriately considered as a species complex. There are few records of this species from regions other than peninsular Thailand, apart from that of Lekagul & McNeely (1977) from Chiengmai, or Chiang Mai, northwest Thailand (as *C. fuliginosa* and *C. dracula*). Furthermore, there are no specimens of *C. fuliginosa* from Thailand, other than peninsular Thailand, in the collection of The Natural History Museum, while in the collection of the American Museum of Natural History there are single specimens from Nakhon Nayok, Khao Yai National Park and Nakhon Ratchasima, central Thailand, plus an unconfirmed specimen from Umphang, western Thailand. In the current survey, *C. fuliginosa* was identified from prey remains of the carnivorous bat, *Megaderma lyra* E. Geoffroy, 1810 collected at Thung Yai–Huai Kha Khaeng Wildlife Sanctuary, western Thailand; however there are only a few fragmentary specimens, dubiously attributed to this species, among the owl pellets from Loei Province. There are similarly few records of *C. attenuata* from Thailand; Lekagul & McNeely (1977) listed this species from Nakhon Phanom and Udon in the northeast, and Chiang Mai, northwest Thailand. There was no evidence

Fig. 4 Lateral view of mandible from top of *C. attenuata*
BM(NH)1911.9.8.26, *C. hilliana* BM(NH)1994.90 and *C.
fuliginosa* BM(NH)1933.4.1.183.

Fig. 5 Lateral view of left anterior dentition. Left: upper toothrow
(I^1 to P^4); right: lower toothrow (I_1 to P_4). Top: *C. attenuata*
BM(NH)1911.9.8.26; middle: *C. hilliana* BM(NH)1994.119 upper
toothrow, BM(NH)1994.118 lower toothrow; bottom: *C.
fuliginosa* BM(NH)1933.4.1.178. Scale 1 mm.

of *C. attenuata* either amongst the owl pellet remains from
Loei Province or from remains found at *M. lyra* roosts in
Thung Yai–Huai Kha Khaeng. It is therefore uncertain if *C.
hilliana* is sympatric with either *C. fuliginosa* or *C. attenuata*.

Crocidura hilliana does, however, occur sympatrically with
a smaller species of *Crocidura* which proved difficult to
determine from the fragmentary skulls in the owl pellets.
Allen & Coolidge (1940) collected *C. vorax* (currently
grouped with *C. pullata* Miller, 1911 from the Himalayas, see
Hutterer, 1993) from northwestern Thailand, while a speci-
men from Lat Bua Kao, mainland Thailand, attributed to *C.
fuliginosa* by Kloss (1919) is also an example of *C. p. vorax*.
Several skulls attributable to this species were found in the
owl pellets from Loei, while a good series was recovered from
the *M. lyra* prey remains from Thung Yai–Huai Kha Khaeng,
where an additional skull was found in the faeces of a large
carnivore. The only other species of *Crocidura* listed by
Lekagul & McNeely (1977) from mainland Thailand was *C.
horsfieldii indochinensis* from Chiang Mai and Khao Yai
National Park . Most recently, Davison (1984), recorded *C.
monticola* from penisular Thailand. Neither of the last two
species mentioned above were identified from either area,
although pellets from Loei Province contained another shrew
Suncus etruscus (Savi, 1822), plus a variety of rodent and bat
species.

Since there has been so little systematic collection in
Thailand, it is impossible to make categoric statements about
the new species, however it seems likely that it is relatively
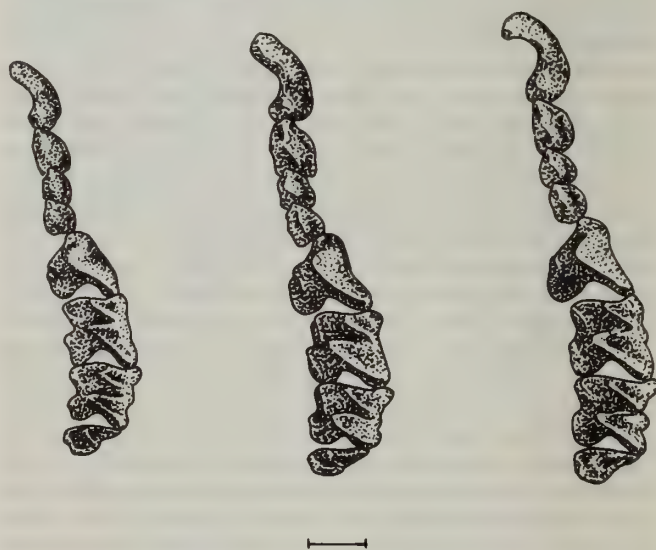localised in its distribution. Even in areas where collecting

Fig. 6 Occlusal view of left upper toothrow from left to right of *C.
attenuata* BM(NH)1911.9.8.26, *C. hilliana* BM(NH)1994.121 and
C. fuliginosa BM(NH)1933.4.1.178. Scale 1 mm.

efforts have been more stringent, shrews are frequently difficult to trap, perhaps giving a false impression of their rarity as faunal components. The discovery of this new species of shrew, apparently present as a sufficiently large population to form an important and regular part of the diet of the resident owls, is therefore not so surprising as it might first appear. Because of the nature of the specimens, even less information than usual is known about the ecology of the new species, although some implications may be drawn from knowledge of the ecology and behaviour of the owls. The barn owl roosting sites of both collecting localities are caves in limestone outcrops in or near temple grounds, surrounded by bamboo and deciduous trees. Individual roost sites at Wat Tham Maho Lan are generally within 0.5 km of cultivated maize fields, while those at Wat Tham Pha Phu are within 1 km of rice and cassava fields. The home range of barn owls in the British Isles and Africa is generally 1–2.5 km, rarely up to 3 km (Bunn *et al*. 1982; Andrews, 1990). Because of this small hunting range, it may be inferred that this habitat which extends for some distance around the roosting site is also the habitat for the shrews on which they prey. Barn owls are nocturnal and crepuscular in their hunting behaviour, the implication being that the shrews are active for at least a proportion of the same activity period.

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Redescription of *Sudanonautes floweri* (De Man, 1901) (Brachyura: Potamoidea: Potamonautidae) from Nigeria and Central Africa

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CONTENTS

SYNOPSIS. The African fresh-water crab *Sudanonautes floweri* (De Man, 1901) is redescribed from the male syntype from Sudan (designated here the lectotype) and a large series of other specimens. The species is recognised by a combination of characters of the carapace, chelipeds, mandibles, and gonopods. *Sudanonautes floweri* is compared to related species occurring in Nigeria and Central Africa. The species is found in guinea and woodland savanna from northern Nigeria to southern Sudan, in tropical rain forest from south-east Nigeria to northern Angola (including Bioko), and along the Zaire river and its tributaries. *Sudanonautes floweri* is one of the second intermediate hosts of the human lung fluke (*Paragonimus*) in Africa.

INTRODUCTION

Recent major works on the taxonomy of the fresh-water crabs of Africa (Bott, 1955, 1959, 1964; Monod, 1977, 1980) recognise three species of *Sudanonautes* Bott, 1955 – *S. aubryi* (H. Milne Edwards, 1853), *S. africanus* (A. Milne Edwards, 1869), and *S. pelii* (Herklots, 1861). Since that time a number of other species in this genus have been added (Cumberlidge, 1991, 1993a, b). The subject of the present work, *S. floweri* (De Man, 1901), was formerly considered by both Bott (1955) and Monod (1977, 1980) to be a subspecies of *S. aubryi*. *Sudanonautes floweri* is judged here to be a good species, and is redescribed from a male syntype from Sudan.

Gonopod 1 of *S. floweri* is distinct (Fig. 2 d-f), and when considered in conjunction with other characters of the carapace and sternum (Fig. 1 a-c) and mandibles (Fig. 2 a-c), can be used to identify the species unequivocally. This is important, since *S. floweri* is one of the four species of *Sudanonautes* that serve as the second intermediate host of the human lung fluke (*Paragonimus*) in Nigeria and Central Africa (Voelker, *et al.*, 1975; Voelker & Sachs, 1977; Nozais, *et al.*, 1980). However, the ambiguous descriptions of *S. floweri* and

S. aubryi in the literature (A. Milne Edwards, 1853; De Man, 1901; Bott, 1955; Monod, 1977, 1980) have led to the misidentification of specimens of *S. floweri* as *S. aubryi* by parasitologists (Voelker, *et al.*, 1975, fig. 6; Voelker & Sachs, 1977, fig. 4).

The right mandible and the right first and second gonopods of the type of *S floweri* were removed to illustrate these structures from different angles and under magnification (Fig. 2 a-i). Specimens of *S. floweri* from Nigeria collected by the author were either dug from their burrows at the sides of streams, or were trapped in fishing nets set overnight in ponds. One specimen (NMU 9.IV.1983) was caught by hand under rocks in a dried river bed, immediately following the temporary damming of the river by villagers. Four measurements, carapace length, carapace width, carapace height, and front width, were recorded from each specimen using digital callipers. Carapace proportions were calculated according to carapace length. These data were pooled and used for descriptions of growth (Fig. 3 a,b). Statistical comparisons between species were made between sexually mature adults only (Table 1). The distribution of *S. floweri* described here is based on the direct examination of a large number of specimens from 73 different localities in 9 countries. Litera-

ture records are generally not reliable, and have not been included.

The following abbreviations are used: AMNH, American Museum of Natural History, New York, NY, USA; FMC, Field Museum, Chicago, IL, USA; MCZ, Museum of Comparative Zoology, Harvard, MA, USA; MNHN, Muséum National dHistoire Naturelle, Paris; NHM, The Natural History Museum, London, UK; NNH, Nationaal Natuurhistorisches Museum, Leiden, The Netherlands; NMU, Northern Michigan University, Marquette, MI, USA; RCM, Royal Congo Museum, Tervuren, Belgium; SMF, Senckenberg Museum, Frankfurt am M., Germany; USNM, The United States National Museum of National History, Smithsonian Institution, Washington, DC, USA; ZIM, Zoological Institute and Museum, Hamburg, Germany; ZMB, Museum für Naturkunde der Humboldt-Universitat, Berlin, Germany; CW = carapace width at widest point; CL = carapace length, measured along median line; CH = cephalothorax height, maximum height of cephalothorax; FW = front width, width of front measured along anterior margin; m = male; f = female; coll. = collected by.

SYSTEMATIC ACCOUNT

Sudanonautes floweri (De Man, 1901)
(Figs 1 a-i, 2 a-j, 3 a,b, Table 1)

Potamon (Potamonautes) floweri; De Man, 1901:94–98, 100–101, pl. X (fig. 1–7); Rathbun, 1904, pl. XVII (figs 2, 6); Rathbun, 1905:193–195; Rathbun, 1921:406–410, fig. 6, pl. XX (fig. 2); Parisi, 1925:99.
Potamon (Potamonautes) aubryi; Balss, 1914, p. 405 (except ZIM K13557 from Mukonje farm, Cameroon, not Potamon aubryi H. Milne Edwards, 1853).
Potamonautes floweri; Balss, 1936:171, fig. 6.
Potamon floweri; Flower, 1931:734; Chace, 1942:211; Capart, 1954:834, fig. 21.
Sudanonautes (Convexonautes) aubryi floweri; Bott, 1955:304–306, fig. 65, 100, a-b, pl. XXVIII (fig 2 a-d); Monod, 1977:1218; Monod, 1980:384–385.

DIAGNOSIS. Mandibular palp 2-segmented; terminal segment single, undivided, with small hard, hair-fringed flap at junction between segments (Fig. 2 a-c). Terminal segment of gonopod 1 with raised lobe on cephalic part, separated from caudal part by a conspicuous longitudinal groove; subterminal segment of gonopod 1 distinctly broadened on outer margin (Fig. 2 d-f). Conspicuous raised ridges on sternum at points where chelipeds articulate (Fig. 1 c). Carapace greatly arched (CH/CL = 0.61, Fig. 1 b), very wide (CW/CL = 1.51, Fig. 1 a). Vertical suture separating sub-branchial and suborbital regions meeting anterolateral margin at base of intermediate tooth (Fig. 1 b).

DISTRIBUTION. Nigeria, Cameroon, Bioko (= Fernando Po), Central African Republic, Sudan, Zaire, Congo, Gabon, Cabinda, Angola. It is likely that S. floweri is also present in Equatorial Guinea. Rathbun (1921) and Balss (1936) provided details of the distribution of the species in Zaire. Monod (1980) reported S. floweri from the basins of the Nile, Zaire, Chari, and Lake Chad. The present work adds several new localities in Nigeria, Bioko, and northern Angola.

MATERIAL

LECTOTYPE. NHM reg. 1901.8.26.2, 1m (CW 48.5, CL 30.5, CH 17.8, FW 11.7 mm), from Bahr el Gebel, Sudan, coll. Capt. S. S. Flower, 26.viii.1901. This specimen is here designated the lectotype of S. floweri. De Man did not specify types, so the material he examined was syntypic.

OTHERS. The catalogue number of material held at NHM and NMU begins with the date (year, month, day) of collection or acquisition. NIGERIA. NHM 1895.5.5.1–4, Asaba, 150 miles up the Niger, coll. N. H. Crosse. NHM 1905.6.5.98–100, Sapele, junction of Jameson and Aethiop rivers, coll. Dr. Ansoroye. NHM 1910.4.30.19–22, Oban southern Nigeria, coll. P. A. Talbot. NHM 1938.7.1, Obubra, southern Nigeria, coll. I. Sanderson. RCM 52.889, Jos, 1967, coll. E. B. Guong. NMU 8–12.V.1975, Rosse, at Iguoriokhi, Bendel State, 1f, 8–12.v.1975, coll. Bruce Powell. NMU 24.IV.1980, first or second roadside culvert, Calabar, 1f (CW 45.5 mm) dug from burrow, coll. J. C. Reid. NMU 30.IV.1982, Ogoja, Cross River State, 1m, CW 50 mm, dug from hole at edge of swamp at Ogoja, rain forest/ woodland savanna, coll. B. D. Barrett. NMU 4.I.1983, Kaduna river (year-round flow), Kaduna State, 4m, coll. Fatima Abdulkadir. NMU 1.III.1983, dug from holes, Kaduna, Kaduna State, coll. Fatima Abdulkadir. NMU 4.IV.1983, foot of Obudu plateau, Cross River State, 1m, fast white water, big rocks, small rocks, sand gravel bottom, caught by villagers, who dammed stream, dried river bed, caught crabs under rocks, (with S. africanus, S. granulatus), coll. N. Cumberlidge. NMU 12.XII.1983, Yankari Game Reserve, Bauchi State, Hippo Pool, dug from holes, 1m, 1f, coll. N. Cumberlidge. NMU 30.IV.1984, pond near tributary of river Niger (20 km east of river), Otta, Benue State, 1f, (CW 54 mm), coll. John Iyage. NMU 12.VI.1984, dug from holes in banks of river Samu, tributary of Niger, Pasakwauri, near Kagoro, Kaduna State, 1m, 1f, coll. N. Cumberlidge. ZIM K3484, Benin, 1m, 2f, xii.1909, coll. C. Manger. ZIM K30252, Njaba creek, 15.iii.1973, coll. J. Voelker. ZIM K30314, Cross river, near Arochukwu, 6.iv.1974, coll. J. Voelker. CAMEROON. NHM 1938.7.1.9–13, Mamfe, coll. I. Sanderson. NHM 2.VIII.1968, Kindongo, south Bakundu, west Cameroon, in hole on forest floor about 100 yds from nearest (non-permanent) water, coll. T. S. Jones. RCM 54.190, Kombetiko, 5 km from Batouri, river Tanadi, 3 specimens, 2.ii.1976, coll. F. Puylaert. RCM 53.389, Olounou, 15–30 specimens, 15–17.viii.1971, coll. F. Puylaert. RCM 54.198, Bissiri Mayerey, 20.i.1976, coll. F. Puylaert. SMF 2098, Bibundi, 20.viii.1948, coll. Justus Weil. SMF 2868, Bibundi, coll. Justus Weil. SMF 1787, Victoria, 1907, O. Valley. NMU 24.X.1970, near Mamfe, crossing road by Baduma village, Kumba-Mamfe road, 1f, coll. R. H. L. Disney. ZIM K3526, 1m, 1f, 24.xii.1911, coll. Dr. E. Fickendey. ZIM K25447, Duala, 1m, 4.x.1912, C. Manger. ZIM K30397, Kembong, near Mamfe, 26.iv.1975, coll. J. Voelker. ZMB 5552, Djeerfluss, 1m, coll. Schweinfurth. ZMB 7789, Benue, 4–9.viii.1889, coll. Staudinger. ZMB 8234, Barombi Lake, 1f, coll. Zeuner. ZMB 10023, 1f, coll. Preuss. ZMB 10216, Johann Albrechtshöhe (modern name unknown, 4°40'N, 9°20'E), 1f, coll. Conradt. ZMB 13718, Victoria, 1f, coll. Deutsche Tiefsee Expedition. ZMB 14342, Douala, 2f, 5.xi.1910, coll. Shaeffer. ZMB 16440, Barombi Station, 1m, 1891, coll. Preuss. ZMB 16947, Douala, 1m, coll. Thorbeke.

ZMB 20161, Buea, 6f, 16.xi.1892, coll. Preuss. ZMB 20195, Buea, 1m, 1f, coll. Preuss. ZMB 20199, Victoria, 4m, coll. Preuss. ZMB 21300, river Sanaga, Douala grassland district, 1200 m, 1m, 11.i.1917, coll. Elbert. ZMB 21308, Douala, 1f, coll. Thorbeke. CENTRAL AFRICAN REPUBLIC. RCM 55.399, Giako river, Bougua, 26.ii.1982, coll. L. de Vos & J. Kempeneeus. RCM 53.086, near Bangui, 22.xii.1967. SUDAN. NHM 1912.12.31.52, Nyonki Nile, 2030 feet, 1f, hatchlings, 28.iv.1912, coll. Sir F. T. Jackson. NHM 1912.12.31.53, Gondokoro, 1800 feet, 12.iv.1912, coll. Sir F. T. Jackson. NHM 1913.9.10.1–3, Lado Nipo, 15 miles north of Kojokaji, coll. S. S. Flower, zoological survey of Egypt. NHM 1913.9.10.9–10, new cut to Zeraf, north of Shamfe, coll. G. W. Graham. NHM 1918.12.13.1–3, Mongalla, coll. S. S. Flower, Zoological Survey of Egypt. NHM 1922.11.22.7–11, Mongalla, Kanisa, vi.1914, coll. S. S. Flower, Zoological Survey of Egypt. FMC, 400 miles west of Juba, 7m, 18f, 22.xii.1884. ZAIRE. RCM 1666, Buta, 1934, coll. F. Hutsebout. RCM 1.661–1.665, Bambesa, 1.viii.1924, coll. J. Brejko. RCM 47.495, Epulu, ix.1956, coll. Dr. M. Poll. RCM 46.159–46.160, Ngense, 1955. RCM 46.161–46.162, Ngense, 1955. MNHN BP5049, river Dougou, affluent of Uele, 1m, coll. L. Didier, Mission du Bourg Bozas, 1903. MCZ 10612, Faradje, 1m 1f, 21–23.ix.1915. SMF 2405, Luki, coll. E. Dartevelle. SMF 2398, Ganda Sundi, coll. E. Dartevelle. SMF 2385, Faradje, upper Uele, v.1925, coll. Dr. Schoudeten (exchange, RCM 1083, 1079). SMF 2383, Bambesa, coll. Krydag. SMF 1782, Duma, coll. Telinbotz. All of the following AMNH material coll. H. Lang, J. Chapin, AMNH Congo Expedition. AMNH 3338, Faradje, 5m, 2f. AMNH 3339, Faradje. AMNH 3355, Faradje, 3m. AMNH 3357, Faradje, 3m, 1f, x.1912. AMNH 3358, affluents of Nepoko river, near Gamangui (Ituri Forest), 3m, 1f. AMNH 3359, Banana, 3m. AMNH 3359, Poko, 1m, 4f, x–xii.1913. AMNH 3377, affluents of Nepoko river, near Gamangui (Ituri Forest), 3m, 1f. AMNH 3406, south of Poko, x–xii.1913. AMNH 3409, affluents of Nepoko river, near Gamangui (Ituri Forest), 1m. AMNH 3422, Van Kerckhoverville, 2m, 1f, iv.1912. AMNH 3448, Faradje, 1f, 1911. AMNH 3453, Poko, 1m, 4f, viii.1909. AMNH 3458, north of Ganza, 1f (ovig), 16.xii.1909. AMNH 3462, affluents of the Tshope river, near Stanleyville. AMNH 3465, Yakukuku, 1m; Garamba, 1f, xi.1911. BIOKO. NHM 1905.7.19.12, coll. Fernando Po Exploration Committee. ZMB 20164, 1m, 1f, vii.1900, coll. Conradt. GABON. NHM 1908.6.2.22, Lambarene, Ogoué river, coll. M. Ansorge. NHM 1908.6.2.23–24, Abanga river, Ogoué river. NHM 1908.6.2.25, Fang forest, Ogoué river, caught on a mountaintop during heavy tropical rain, 29.iv.1907. NHM 1908.6.2.25a, Masoma river, Ogoué river. AMNH 3367, Libreville, 5m, 5f, ii.1916, coll. H. Lang, J. Chapin. AMNH 3369, 3m, 2f, 1916, coll. H. Lang, J. Chapin. FMC, Gabon or Middle Congo, French Equatorial Africa, 1951–1952, coll. H. A. Beatty. CABINDA. MNHN BP5048 (1m, CW 54.7, CL 36.0 mm), BP5047 (1f, CW 56.6, CL 39.5 mm) Landana, Cote de Loango, 4.ix.1898, coll. M. Petit. ANGOLA. NHM 1912.4.2.1–3, Luali river.

DESCRIPTION OF MALE LECTOTYPE

CARAPACE (Fig. 1 a,b). Ovoid, extremely wide, widest in anterior third (CW/CL = 1.51), extremely high, with maximum height in anterior region (CH/CL = 0.61). Anterior margin of front straight, curving under, front relatively narrow, about one-quarter carapace width (FW/CW = 0.25). Surface of carapace smooth with no deep grooves. Postfrontal crest consisting of fused epigastric, postorbital crests, lateral ends with slight crenulations; mid-groove broad, shallow. Postfrontal crest contrasting colour to carapace, located very close to, almost touching, postorbital margin; laterally, postfrontal crest meeting, or nearly meeting, anterolateral margin of carapace at, or near, epibranchial tooth. Exo-orbital tooth blunt, low, intermediate tooth smaller than exo-orbital tooth, epibranchial tooth small, low, a granule. Anterolateral margin of carapace raised and granulated, bigger granules at epibranchial corner, smaller granules behind, continuous with posterolateral margin, or curving slightly inward in hepatic region. Posterior margin about two-thirds as wide as carapace width.

Face of of carapace with 2 sutures, 1 longitudinal, 1 vertical, dividing face and sides into 3 parts (Fig. 1 b). Longitudinal suture dividing suborbital, subhepatic regions from pterygostomial region, beginning under inferior medial margin of orbit, and curving backward across side. Short, curving, vertical suture dividing suborbital region from subhepatic region (Fig. 1 b); suture beginning beneath intermediate tooth, curving down to meet longitudinal suture, marked by row of small rounded granules. Third maxillipeds (Fig. 1 d) filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped; ishium of third maxilliped smooth, with faint vertical groove; merus with flanged edges. Mandibular palp 2-segmented, terminal segment single, undivided, small hard, hair-fringed flap at junction between segments (Fig. 2 a-c).

PEREIOPODS (Fig. 1 f-i). Chelipeds of lectotype unequal, right longer, higher than left. Dactylus of right cheliped not arched, fingers enclosing long interspace when closed, palm of propodus swollen. Fingers of right cheliped with 4 larger teeth on lower digit and 4 larger teeth on upper digit, interspersed with a series of smaller pointed teeth along their lengths. Inferior margins of merus with rows of small teeth, cluster of granules surrounding larger tooth at distal end. Carpus of cheliped with 2 large pointed teeth on inner margin, second smaller than first. Left cheliped similar to right, but smaller in all respects. Walking legs (pereiopods 2–5) slender (Fig. 2 j), third pair longest, fourth pair shortest. Posterior margin of propodus of walking legs serrated, dactyli of walking legs tapering to point, each bearing rows of downward-pointing sharp bristles; dactylus of fourth pair shortest (Fig. 2 j).

UNDERSIDE. First transverse groove on sternum (between sternal segments 2 and 3) complete; second groove (between sternal segments 3 and 4) consisting of 2 small notches at sides of sternum; sternum with conspicuous raised ridges at points where chelipeds insert (Fig. 1 c). Segments 1–6 of abdomen four sided, last segment triangular, sides indented, rounded at distal margin (Fig. 1 e); segment 3 broadest, segments 3–7 tapering inwards (Fig. 1 e).

Terminal segment of gonopod 1 long (2/3 as long as subterminal segment), first half straight continuation of subterminal segment, second half curving outward, tapering to pointed tip; terminal segment with raised lobe on the cephalic part, separated
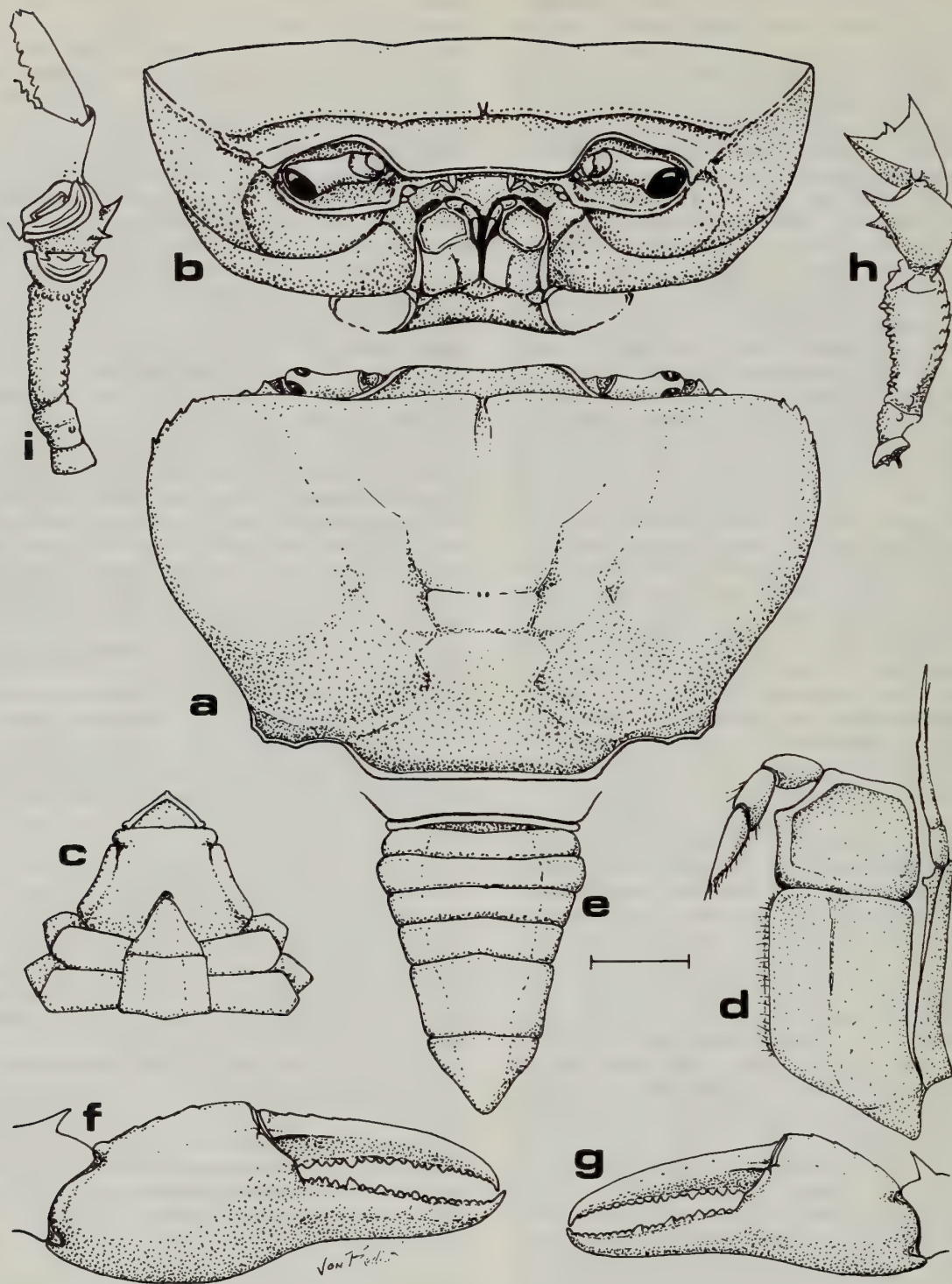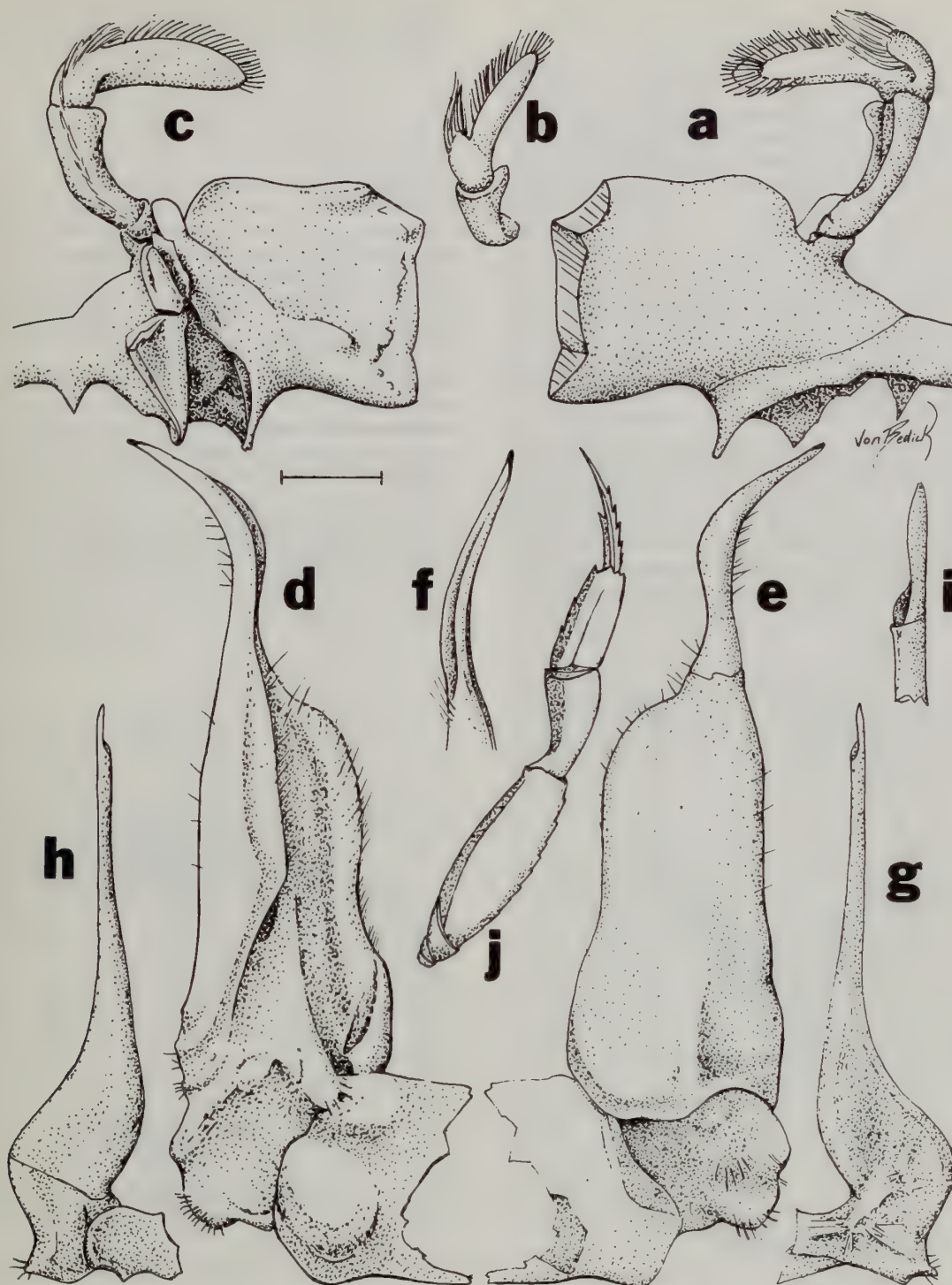
Fig. 1 *Sudanonautes floweri*, lectotype, adult male from Bahr el Gebel, Sudan (CW 48 mm), NHM reg 1901.8.26.2. (a), whole animal, dorsal aspect; (b), carapace, frontal aspect, (c) sternum; (d) left third maxilliped; (e), abdomen; (f), right cheliped, frontal view; (g), left cheliped, frontal view; (h) carpus, and merus of right cheliped, superior view; (i) carpus, and merus of right cheliped, inferior view. Scale bar equals 15 mm (h, i), 10 mm (c, f, g), 7.5 mm (a, b, e), and 3.75 mm (d).

from the caudal part by a distinct longitudinal groove visible from caudal and superior views (Fig. 2 d,f), not visible from cephalic view (Fig. 2 e). Subterminal segment of gonopod 1 broadened conspicuously on outer margin, fringed with bristles (Fig. 2 d,e), with raised flap extending halfway across segment in distal part, tapering diagonally to point at junction with terminal segment, forming roof of chamber for gonopod 2; subterminal segment beneath flap forming lower floor of chamber for gonopod 2 (Fig. 2 d). Gonopod 2 (Fig. 2 g-i) shorter than gonopod 1 (reaching only to the junction between last 2 segments of gonopod 1).

Fig. 2 *Sudanonautes floweri*, lectotype, adult male from Bahr el Gebel, Sudan (CW 48 mm), NHM reg 1901.8.26.2. (a), right mandible anterior view; (b), right mandible superior view; (c), right mandible posterior view; (d), left gonopod 1, caudal view; (e), right gonopod 1, caudal view; (f), right gonopod 1, superior view; (g), right gonopod 2, cephalic view; (h), right gonopod 2, caudal view; (i), right gonopod 2, caudal view, detail of terminal segment; (j) left pereiopod 2. Scale bar equals 10 mm (j), 1.5 mm (a-c, d-h), and 0.5 mm (i).

Terminal segment gonopod 2 cup-shaped, with pointed tip, extremely short, only 1/15 as long as subterminal segment. Subterminal segment gonopod 2 widest at base, then tapering sharply inward, forming long, thin, pointed, upright process supporting short terminal segment.

ADULT FEMALE. Right, left chelipeds same proportions as male of same size, unequal in both length, height. Mature female abdomen very wide reaching coxae of pereiopods 2–5. Segments of female abdomen becoming gradually longer distally, first, fifth becoming gradually wider, abdomen being

widest at groove separating fourth, fifth segments. Sixth segment, telson together forming near semicircle.

GROWTH (Fig. 3 a,b, Table 1). Measurements and proportions given in Table 1, Fig. 3 a,b. Sexual maturity judged by development of female abdomen: abdomen of mature females overlapping bases of coxae of walking legs, pleopods broad, hair-fringed. Pubertal moult, from pubertal stage to sexual maturity, occurring between CW 33–42 mm. Largest known specimen, (male from Cameroon) CW 60.4, CL 39.9. In Zaire, eggs produced in December; in Sudan, hatchlings present in April. Dimensions of carapace varying with age (Fig. 3 a). Relative proportions of carapace width (CW/CL) and height (CH/CL) of juvenile and pubescent *S. floweri* not significantly different (*P* >0.05) from adults (Fig. 3 b). Front width becoming smaller with age: FW/CL of adult *S. floweri* significantly more narrow (*P* <0.001) than that of juvenile and pubescent animals (Fig. 3 b).

COLOUR. (Living adults from Ogoja, Nigeria). Dorsal carapace dark purplish brown, with a contrasting yellow-orange postfrontal crest and yellow orbital border. Flanks light brown, third maxillipeds pale brown with purple tinge, eyestalks white cream, cornea black, sternum and abdomen light brown with purple tinge. Arthrodial membranes between joints of chelipeds and pereiopods dark brown; dorsal surface

Table 1 Means (± *SE*) of ratio of carapace width (CW), carapace height (CH), and front width (FW), to body size (CL) of adult *Sudanonautes floweri* compared to the adults of six closely related species of *Sudanonautes* from Nigeria and Central Africa.

	CW/CL $X \pm SE$	CH/CL $X \pm SE$	FW/CL $X \pm SE$
Sudanonautes floweri	1.52 ± 0.01	0.61 ± 0.0	10.38 ± 0.003
	(*n* = 65)		
Sudanonautes aubryi	1.37[a] ± 0.01	0.52[a] ± 0.01	0.38 ± 0.002
	(*n* = 63)		
Sudanonautes africanus	1.38[a] ± 0.01	0.43[a] ± 0.003	0.36[c] ± 0.004
	(*n* = 26)	(*n* = 14)	(*n* = 15)
Sudanonautes granulatus	1.42[a] ± 0.01	0.51[a] ± 0.01	0.41[a] ± 0.01
	(*n* = 33)		
Sudanonautes monodi	1.49[a] ± 0.01	0.58[b] ± 0.004	0.39 ± 0.004
	(*n* = 23)		
Sudanonautes kagoroensis	1.52 ± 0.02	0.50[a] ± 0.01	0.39 ± 0.004
	(*n* = 9)		
Sudanonautes orthostylis	1.45[a] ± 0.02	0.51[a] ± 0.01	0.46[a] ± 0.01
	(*n* = 10)		

Proportion significantly different from that of *S. floweri*: [a] = *P* <0.001; [b] = *P* <0.01; [c] = *P* <0.05.
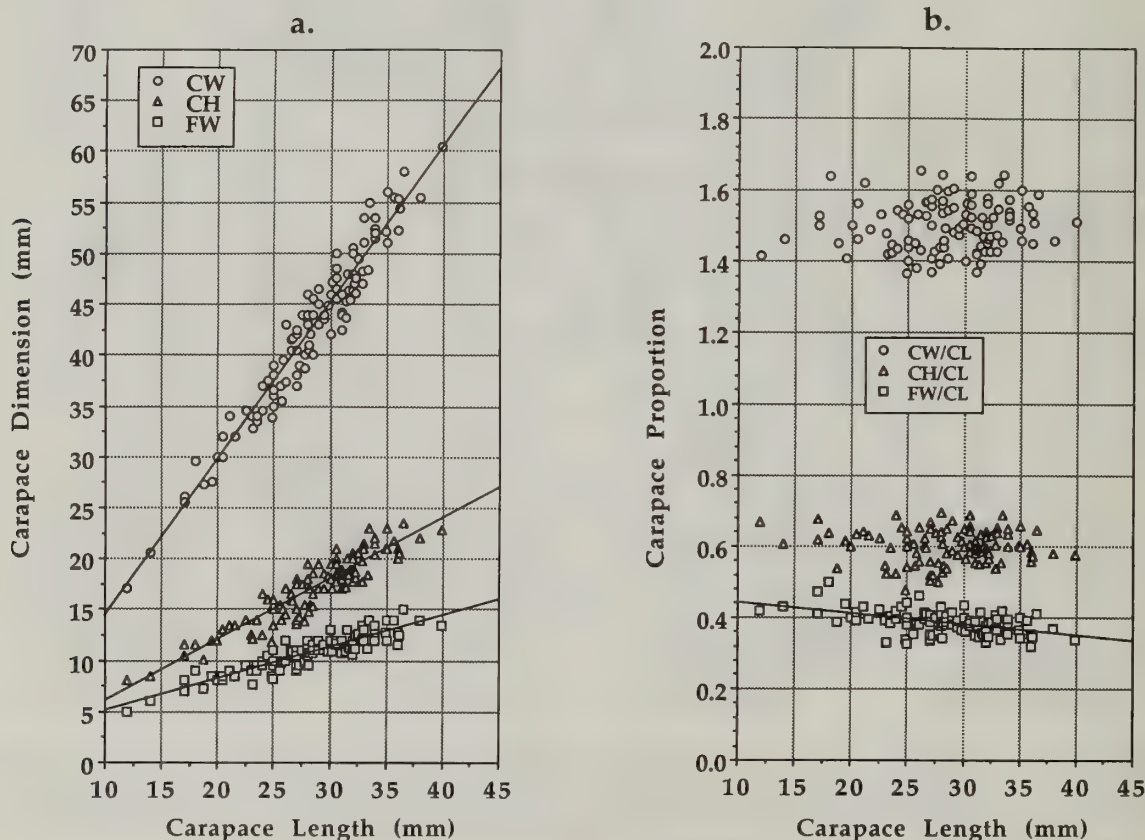
Fig. 3. Comparisons of 108 specimens of *Sudanonautes floweri*. a, dimensions of the carapace (CW, CH, FW) compared to body size (CL), *r* values (all at *df* = 107) indicate a highly significant correlation (*P* <0.001) between size classes. b, relative proportions of carapace width and height (CW/CL, CH/CL) compared to body size (CL), *r* values (both at *df* = 107) indicate no significant correlation (*P* >0.05) between size classes; relative proportions of front width (FW/CL) compared to body size (CL), *r* value (at *df* = 107) indicates a highly significant correlation (*P* <0.001) between size classes.

of chelipeds and pereiopods light brown, ventral surface light brown. Specimens from the Ogoué river, in the Fang forest, Gabon, with brown-pink carapace, shading into neutral orange in middle; walking legs orange-vermillion.

VARIATION. The anterolateral margin is raised, marked by a series of granules or small teeth in some specimens (from Juba, Shambe, and Kojo-Kaji, Sudan; Ituri forest, Banana, and Faradje, Zaire; and Ogoja, Kaduna, and Bendel State, Nigeria). In other specimens (Poko, Zaire; Fernando Po, and Luali, Angola) the anterolateral margin is completely smooth. In specimens from Oban, Nigeria, the anterolateral margin is smooth except for the epibranchial tooth (which is the size of a large granule), followed by two smaller granules. It is possible that the above variations of the anterolateral margin are due to changes associated with growth. For example, the adult male (CW 53.5 mm) from Juba, Sudan (FMC) was the only one in which the anterolateral margin was smooth out of 25 specimens of all sizes. This margin was toothed or serrated in all the other specimens which measured CW 48 mm or less. A similar observation was made in the series of specimens from Cameroon (RCM 53.389), where the anterolateral margin of a large male (CW 60.4 mm) was completely smooth, but that of smaller specimens was granulated. Some specimens from Juba, Sudan, had serrations on the dorsal surface of the dactylus of the cheliped while other specimens from Juba, and from Nepoko, Zaire, lacked these serrations.

ECOLOGICAL NOTES

Sudanonautes floweri is a common species of fresh-water crab widely distributed in Nigeria and Central Africa. It is found in the moister regions of the woodland and guinea savanna zones from central Nigeria to southern Sudan. This species is also found in the humid tropical rain forest habitats in south-east Nigeria, south Cameroon, Bioko, Central African Republic, Zaire, Congo, and Gabon. In Nigeria, *S. floweri* occurs in the drainage basins of the lower Niger, Benue and Cross rivers. Specimens collected from Yankari Game Reserve, Bauchi State, Nigeria were dug from holes at the base of tufts of tall grass clumps in a marsh at the confluence of rivers Yashi and Gaji, an area heavily trampled by big game, especially elephants. Many specimens of *S. floweri* were caught on land during heavy tropical rain.

In Sudan, *S. floweri* lives both in the Yei river basin (a tributary of the Nile), in the mountainous watershed between the Nile and the Zaire rivers, and in the level papyrus swamps (Flower, 1931). In Zaire, *S. floweri* has been reported from the lower and middle reaches of the Zaire river, and in the Ubangi and Uele rivers (Rathbun, 1921). The habitat of *S. floweri* in Zaire has also been described by Rathbun (1921), who summarised the field notes of Herbert Lang. *S. floweri* was often found in heaps of rotting vegetation in water courses, and Lang speculated that this habit may carry the crabs downstream, explaining (at least in part) the wide distribution of this species. Predators of *S. floweri* in the rain forests of Zaire include crocodiles, monitor lizards (*Varanus niloticus*), insectivorous otter shrews (*Potamogale velox*) and several small carnivores, chiefly species of mongooses and the African civet (*Viverra civetta*).

Sudanonautes floweri is common in shallow streams, rivers, and ponds, and digs burrows near waterways. This species is also found on land either next to water or some distance away, since it is capable of breathing air, and functions well for long periods out of water. The widened and highly arched carapace, and the lack of teeth on the anterolateral margins of the carapace of *S. floweri* are features often associated with air-breathing and burrow-living. This body shape contrasts with the more flattened, deep-grooved, and spiny carapace of the more aquatic river-living species such *S. faradjensis* (Rathbun, 1921).

TAXONOMIC REMARKS

The difficulties in distinguishing between *S. aubryi* and *S. floweri* date back to the work of Rathbun (1904, 1905). Although Rathbun (1905) described *S. floweri* and *S. aubryi* as separate species, her description of *P. (P.) aubryi* was based largely on specimens of *S. floweri*. Specimens from Cabinda (MNHN B5048) and Zaire (BP 5049) used by Rathbun (1905) to describe *S. aubryi* have been examined in the present study and found to be *S. floweri*. This opinion is supported by the photographs of the specimens from Zaire and Gabon provided by Rathbun (1904: TVI, plate IX, figs 5, 8) which closely resemble *S. floweri*, and which are clearly different from the photograph of the female type of *S. aubryi* (Rathbun, 1904: TVI, plate IX, fig. 3). Unfortunately, Rathbun's (1905) ideas were accepted by later workers with the result that the descriptions of *S. aubryi* in Balss (1914, 1929), Capart (1954), Bott (1955) and Monod (1977, 1980) all refer to *S. floweri* rather than to *S. aubryi sensu* H. Milne Edwards (1853).

COMPARISONS. Six species of *Sudanonautes* are sympatric with *S. floweri* in Nigeria and Central Africa, viz. *S. granulatus* (Balss, 1929), *S. kagoroensis* Cumberlidge, 1991, *S. orthostylis* Bott, 1955, *S. monodi* (Balss, 1929), *S. aubryi*, and *S. africanus*. These taxa can be distinguished from *S. floweri* as follows. The small hard flap on the mandibular palp at the junction between the two segments (Fig. 2 a-c), and the conspicuous raised ridges on the sternum at the points where the chelipeds insert (Fig. 1 c), distinguish *S. floweri* from all other species of *Sudanonautes*, which lack these features.

In addition, the raised lobe on the cephalic part of the terminal segment of gonopod 1, separated from the caudal part by a conspicuous longitudinal groove in *S. floweri* (Fig. 2 d,f) is also shared, in varying degrees, by *S. monodi*, *S. kagoroensis* and *S. granulatus*. These three species can be further distinguished from *S. floweri* by the following characters. The raised lobe on the cephalic part of the terminal segment of gonopod 1 of *S. monodi* (Cumberlidge, 1991) is considerably higher than that of *S. floweri*. In addition, the carapace of *S. monodi* is significantly ($P < 0.001$) flatter (CH/CL *S. monodi* = 0.52, *S. floweri* = 0.61), and less wide (CW/CL *S. monodi* = 1.37, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). *Sudanonautes monodi* has patches of granules on the anterior corners of the carapace behind the postfrontal crest, while *S. floweri* lacks these granules. Finally, *S. monodi* is found in dry sudan savanna from Nigeria to Sudan, while *S. floweri* is absent from this region; and *S. monodi* is absent from woodland savanna and rain forest where *S. floweri* is abundant.

Sudanonautes kagoroensis was described by Cumberlidge

(1991), and can be distinguished from *S. floweri* by examination of gonopod 1: the raised lobe on the cephalic part of the terminal segment in *S. kagoroensis* is lower than that in *S. floweri*, and the outer margin of the subterminal segment of gonopod 1 is slim, while that of *S. floweri* is conspicuously broadened (Fig. 2 d, e). Furthermore, the carapace of *S. kagoroensis* is significantly (P <0.001) flatter (CH/CL = 0.44) than that of *S. floweri* (CH/CL = 0.61).

Sudanonautes granulatus was redescribed by Cumberlidge (1993a) and can be distinguished from *S. floweri* as follows. The carapace of *S. granulatus* is significantly (P <0.001) flatter (CH/CL *S. granulatus* = 0.51, *S. floweri* = 0.61), and less widened (CW/CL *S. granulatus* = 1.41, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). In addition, the dactylus of the major cheliped of the adult male of *S. granulatus* is dramatically arched, while that of *S. floweri* is only moderately arched; the major cheliped of adult male *S. granulatus* is as long as, or longer, than the carapace width (Cumberlidge, 1993a), whereas that of *S. floweri* is shorter (Fig 1 f) than the carapace width (Fig. 1 a,b).

Three other species, *S. aubryi*, *S. africanus*, and *S. orthostylis*, differ from *S. floweri* in that the terminal segments of gonopod 1 of these species lack both a raised cephalic lobe, and a distinct longitudinal groove in the caudal view. These three taxa can be further distinguished from *S. floweri* as follows. The carapace of *S. aubryi* is significantly (P <0.001) flatter (CH/CL *S. aubryi* = 0.52, *S. floweri* = 0.61), and less wide (CW/CL *S. aubryi* = 1.37, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). In addition, the carapace and postfrontal crest of *S. aubryi* are a green-brown colour, whereas these parts of *S. floweri* are uniformly red-brown with a contrasting yellow postfrontal crest.

The terminal segment of gonopod 1 of *S. africanus* is thin and needle-like, while that of *S. floweri* (Fig. 2 d) is wider and has a distinct groove in the caudal view. The carapace of *S. africanus* is significantly (P <0.001) flatter (CH/CL *S. africanus* = 0.43, *S. floweri* = 0.61) and less wide (CW/CL *S. africanus* = 1.38, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). The carapace of *S. africanus* has patches of raised warts, while that of *S. aubryi* is completely smooth. Finally, the pollex of the propodus of the major cheliped of *S. africanus* has a large and conspicuously flattened tooth, which is lacking in adult *S. floweri*.

Sudanonautes orthostylis was redescribed by Cumberlidge (1993b), and can be distinguished from *S. floweri* as follows. The terminal segment of gonopod 1 of *S. orthostylis* is straight, lacks a visible groove, and curves outwards sharply only at the tip, while that of *S. floweri* bears a longitudinal groove and curves from the mid point (Fig. 2 d). The carapace of *S. orthostylis* is significantly (P <0.001) flatter (CH/CL *S. orthostylis* = 0.51, *S. floweri* = 0.61), and less wide (CW/CL *S. orthostylis* = 1.44, *S. floweri* = 1.51) than that of *S. floweri* (Table 1). The frontal margin of *S. orthostylis* is significantly (P <0.001) wider than that of *S. floweri* (FW/CL *S. orthostylis* = 0.46, *S. floweri* = 0.38, Table 1). The dactylus of the major cheliped of *S. orthostylis* is broad and flat, while that of *S. floweri* is narrow. Finally, *S. orthostylis* is a much smaller species, maturing at CW 22 mm, compared to maturity between CW 33–42 mm in *S. floweri*.

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Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fishes, and its phylogenetic significance

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SYNOPSIS. A survey of acanthomorphs reveals that *epaxialis* attachments to distal radials or the distal tips of proximal-middle pterygiophores have a relatively restricted distribution. Four basic morphotypes are recognized: Type 0 – no distal insertions of *epaxialis* (lampridiforms, polymixiiforms, basal paracanthopterygians, zeiforms, beryciforms, smegmamorphs, pleuronectiforms and many perciforms); Type 1 – partially separate *epaxialis* slip(s) inserting on to dorsoposterior and dorsolateral processes of proximal-middle and/or distal radials (batrachoidids [Paracanthopterygii], scorpaeniforms, and among perciforms in blennioids, most cirrhitoids, apogonids, centrogeniids, latine centropomids, grammatids, haemulids, percids, serranids, champsodontids and cheimarrhichthyids); Type 2 – insertions of *epaxialis* to distal portions of pterygiophores without separate slips (possibly basal tetraodontiforms, various perciform taxa including callionymoids, notothenioids, zoarcoids, and some cirrhitids, labrids, percoids and trachinoids); Type 3 – completely separate slip of muscle dorsal to the main body of the *epaxialis* inserting on to anterior pterygiophore shaft with dorsal insertions on to more posterior spine-bearing pterygiophores, and the first ray-bearing pterygiophore, then becoming continuous with the *supracarinalis posterior* (percoid family Mullidae). Type 0 is considered to be plesiomorphic, and the remaining morphologies apomorphic. Their phylogenetic significance is discussed in the context of other characters. Among our conclusions, the Scorpaeniformes is awarded subordinal status within the Perciformes, and the centropomid Latinae is given full familial status.

INTRODUCTION

Within the last five years, there has been renewed interest in higher relationships among acanthomorphs. The recent publication of the Symposium on Phylogeny of Percomorpha (Johnson & Anderson, 1993) and other contributions (Stiassny, 1990; Stiassny & Moore, 1992) have shifted the focus somewhat from phylogenetic work on individual families to broader studies involving interrelationships of suborders and orders. Such studies are hampered by the difficulties inherent in examining large numbers of taxa, determining appropriate character complexes, and interpreting homologies among the variation within those complexes. In many instances, characters are too complex or difficult to survey resulting in an incomplete understanding of their distribution within the included groups. During the course of investigations on the relationships among pseudochromoids (sensu Mooi, 1990), we began surveying the relation of dorsal epaxial myology to the dorsal-fin pterygiophores. Dorsal epaxial myology appears to exhibit limited but sufficient variation over a broad range of taxa and the character states are simple enough to suggest it to be of high potential for phylogenetic analysis of higher relationships among acanthomorphs.

Epaxial muscles, the dorsal component of the body musculature, have received little attention from fish systematists. Although some studies have used variation in the anterior insertions of epaxial slips on to the head (e.g., Mooi, in press;

Stiassny, 1990), few workers using myological features have surveyed this muscle group (Winterbottom, 1974a for a review). Mok *et al.* (1990) were the first to report variation in the relationship of the epaxial musculature with the dorsal-fin pterygiophores. They found that in two percoid families, the Grammatidae and Opistognathidae, the epaxial muscles insert on to the distal portions of anterior dorsal-fin pterygiophores, and interpreted this as evidence for uniting the two taxa as sister groups.

Our continuing studies on the phylogenetic positions of the Grammatidae, Opistognathidae and other pseudochromoid families have failed to provide corroborating evidence for a sister-group relationship between the Grammatidae and Opistognathidae. Moreover, a preliminary survey of epaxial morphology in perciforms revealed that the reportedly unique association of epaxial musculature with dorsal-fin pterygiophores described by Mok *et al.* (1990) is more widely distributed (Gill & Mooi, 1993: 333). Here we present an extensive survey of acanthomorph taxa, and show that, despite having a wider distribution than indicated by Mok *et al.*, epaxial muscle/dorsal-fin pterygicphore associations nevertheless appear to be relatively restricted within acanthomorphs, and exhibit a number of recognizable morphologies. We explore the possible phylogenetic significance of the distribution of epaxial muscle insertions to dorsal-fin pterygiophores and their homology.

METHODS AND MATERIALS

Epaxial musculature/dorsal-fin pterygiophore associations were studied in alcohol-stored specimens. An incision was made through the skin along the length of the fish between one third to one half the distance from the base of the dorsal fin and the midlateral septum. The incision ran from the skull to beneath the segmented-ray portion of the dorsal fin. The skin was either removed or folded dorsally to expose the underlying muscle. The *inclinatores dorsales* usually lifted up with the skin, or were removed individually to permit examination of the epaxial muscles and the dorsal portions of the pterygiophores. When appropriate, epaxial fibres were traced anteriorly or posteriorly to ascertain their association with the *supracarinalis* muscle system. The insertions of epaxial fibres to pterygiophores were often re-examined on cleared and stained specimens and dry skeletons in the collections of the American Museum of Natural History, Milwaukee Public Museum, National Museum of Natural History, and The Natural History Museum. These specimens are not listed in Table 1. Illustrations of muscles were made with a camera lucida attached to a binocular dissecting microscope.

Material dissected for myological observations is listed in Table 1. All species examined during the study are represented in this list, although in many cases, multiple specimens were examined, occasionally from different lots, and sometimes from museum collections other than those listed, particularly the Field Museum of Natural History and Royal Ontario Museum. A complete list can be provided by the authors. Institutional codes follow Leviton *et al.* (1985).

RESULTS

Many (if not most) fishes have some epaxial fibre insertion near the proximal ends or near the middle of the dorsal-fin pterygiophores, whereas some taxa have epaxial muscle insertions on to the distal ends of the pterygiophores. We recognize four morphotypes of epaxial musculature, Types 0 to 3. The consecutive numbering of the morphological types is not meant to imply character transformations; the morphotypes do not necessarily form a polarized transformation series. The vast majority of acanthomorph fishes (including putative basal taxa) exhibit an apparently primitive condition of the epaxial muscles, Type 0, with no attachment to the distal parts of the dorsal-fin pterygiophores, and with the musculature usually lying well below the dorsal tips of the pterygiophores (Fig. 1; Table 1).

Of those taxa that do exhibit insertions on to the distal portions of the pterygiophores, epaxial fibres rarely insert on to pterygiophores other than those bearing non-segmented rays (spines), except where these ray elements are interpreted as secondarily derived from spines (e.g., pseudochromids, zoarcoids, pleuronectiforms). In one scorpaeniform and a perciform genus as discussed below, and probably the paracanthopterygian *Opsanus beta*, there is insertion on primary ray-bearing pterygiophores. Among the taxa with dorsal insertions of epaxial fibres to spine-bearing pterygiophores, there are three recognizable morphologies. Although these morphologies can be defined by specific taxa, their apparent differences become somewhat subjective at the ends of their respective morphological spectra.

Type 1 is characterized by a partially separate muscle mass or series of slips of muscle fibres that insert on to the dorsoposterior and dorsolateral processes of the proximal-middle and/or distal radials of the pterygiophores. At least some fibres originate from the main body of epaxial muscle, but in extreme cases the dorsal muscle mass is detached between successive myosepta, and anteriorly there can be an elongate separate slip of muscle to an anterior pterygiophore (Fig. 2). We observed this morphotype in a single paracanthopterygian species (*Opsanus beta*) (Fig. 3), blennioids, most cirrhitoids, seven percoid families (Apogonidae, Centrogeniidae, Centropomidae, Grammatidae, Haemulidae, Percidae, and Serranidae) and two trachinoid families (Champsodontidae and Cheimarrhichthyidae) among the surveyed perciforms (Figs 1, 4–5, 12–17), and all but one examined scorpaeniform (Figs 6–8) (Table 1).

Among examined scorpaeniforms with Type 1, *Normanichthys crockeri* exhibits a unique morphology (Fig. 8). The epaxial muscles insert on to the lateral processes of the first nine or ten pterygiophores as a separate mass of muscle. Posterior to the first dorsal fin, epaxial fibres attach directly to spineless (naked) pterygiophores and these fibres are not arranged as a separate muscle mass. A separate muscle mass is also present at the second dorsal fin, with insertions on to those pterygiophores bearing segmented rays. This gradually tapers out posteriorly and merges with the main body of epaxial muscle. Other scorpaeniform and percoid taxa exhibiting Type 1 are quite consistent in their epaxial morphology; even among unusual taxa such as *Aploactis* (a scorpaeniform), which has its dorsal fin placed far anteriorly over the skull, a narrow tendon extends from the epaxial to insert on to the third dorsal-fin pterygiophore. Differences arise in the degree of muscle separation, size of the anterior slip, on to which pterygiophores the muscle inserts, and on to which radials of the pterygiophores the insertion occurs (cf. Figs 2–8).

Species with a Type 2 epaxial morphology lack the obvious separation of the dorsal muscle bundle that inserts on to the distal portions of the pterygiophores, and the anterior slip is always absent. The insertions resemble sheets hanging on a clothes-line, draping from one pterygiophore to the next (Fig. 9). In some taxa, the insertions are primarily via long tendons, and the muscle fibres themselves are relatively distant from the dorsal parts of the pterygiophores (Fig. 10). In most elongate taxa, the muscles are much more dorsally situated and the tendons are not as obvious. This morphology is found in various perciform taxa, including some members of the Cirrhitidae, Labridae, Percoidei, and Trachinoidei, and all of the few examined members of the Callionymoidei, Notothenioidei and Zoarcoidei (Table 1). The Tetraodontiformes have a modified condition of this basic morphology which will be discussed below.

A Type 3 epaxial morphology was found only in the family Mullidae (Fig. 11; Table 1). This type consists of a few epaxial fibres inserting on to an anterior pterygiophore relatively ventrally and on to a lateral wing along the main shaft rather than on to a dorsal posterolateral process. A completely separate slip of muscle sits dorsal to the epaxial muscle and inserts on to the anterior pterygiophore and only the posterior pterygiophores of the first dorsal fin. It extends further posteriorly, inserting on to the first pterygiophore of the second dorsal, and gradually narrows posteriorly, insert-

Table 1 List of taxa examined for epaxial muscle morphology. Morphological types: 0 – no association with distal tips of dorsal-fin pterygiophores; 1 – partially separate muscle block or series of slips of muscle fibers that insert on to the dorsoposterior and dorsolateral processes of the proximal-middle and/or distal radials of the dorsal-fin pterygiophores; 2 – insertions to the distal portions of the pterygiophores without an obvious separation from the main muscle body and with no separate anterior slip; 3 – completely separate slip of muscle dorsal to the main body of the *epaxialis* inserting on to an anterior pterygiophore shaft with dorsal insertions on to more posterior spine-bearing pterygiophores and the first pterygiophore bearing a segmented ray, then becoming continuous with the *supracarinalis posterior*. Orders are listed phylogenetically following Johnson & Patterson (1993); suborders, families, and species are listed alphabetically within orders. *Incertae sedis* genera of Percoidei are listed alphabetically among families.

Taxon, Catalogue No., SL (mm)	Type	Taxon, Catalogue No., SL (mm)	Type
LAMPRIDIFORMES		Poeciliidae	
Veliferidae		*Poecilia mexicana*, MPM 8283, 55.4	0
Velifer hypselopterus, AMNH 49575, 118.0	0	**DACTYLOPTERIFORMES**	
POLYMIXIIFORMES		Dactylopteridae	
Polymixiidae		*Dactylopterus volitans*, USNM 307210, 59.5	0
Polymixia lowei, AMNH 10116, 131.0	0	**PERCIFORMES**	
PARACANTHOPTERYGII		Acanthuroidei	
Aphredoderidae		Acanthuridae	
Aphredoderus sayanus, AMNH 50907, 53.5	0	*Acanthurus triostegus*, USNM 139750, 73.5	0
Batrachoididae		Ephippidae	
Opsanus beta, AMNH 52369, 115.0	1	*Chaetodipterus zonatus*, USNM 131415, 48.9	0
Brotulidae		Scatophagidae	
Dinematichthys sp., USNM 297347, 88.5	0	*Scatophagus argus*, BMNH 1976.4.13:2–7, 48.3	0
Gadidae		Anabantoidei	
Urophycis floridanus, MPM 8409, 76.6	0	Anabantidae	
Lotidae		*Anabas testudineus*, AMNH 13766, 65.0	0
Lota lota, MPM 28380, 100.0	0	Badidae	
Percopsidae		*Badis badis*, USNM 89076, 26.8	0
Percopsis omiscomaycus, MPM 14060, 77.1	0	Belontiidae	
ZEIFORMES		*Belontia signata*, USNM uncat., 64.4	0
Parazenidae		*Macropodus opercularis*, AMNH 10641, 38.7	0
Parazen pacificus, AMNH 29459, 116.5	0	Channidae	
BERYCIFORMES		*Channa arga*, AMNH 79406, 121.0	0
Holocentridae		*C. obscurus*, FMNH 70260, 136.0	0
Myripristis pralinus, USNM 285922, 113.5	0	Nandidae	
Sargocentron vexillarus, MPM 30099, 56.7	0	*Monocirrhus polyacanthus*, USNM uncat., 68.0	0
Trachichthyidae		*Nandus nebulosus*, USNM 230323, 47.7	0
Hoplostethus mediterraneus, AMNH 49700, 117.0	0	*Polycentrus schomburgki*, USNM 226071, 41.7	0
SYNBRANCHIFORMES		Pristolepidae	
Mastacembelidae		*Pristolepis fasciata*, USNM 305711, 75.7	0
Caecomastacembelus congricus, AMNH 6157, 145.0	0	Blennioidei	
Mastacembelus armatus, FMNH 68484, 190.0	0	Blenniidae	
ELASSOMATIFORMES		*Entomacrodus nigricans*, MPM 18256, 55.4	1
Elassomatidae		*Hypleurochilus aequipinnis*, MPM 23034, 28.2	1
Elassoma okefenokee, MPM 28810, 20.5	0	*Ophioblennius atlanticus*, MPM 24880, 52.4	1
E. zonatum, MPM 14480, 28.5	0	*Scartella cristata*, MPM 18231, 62.0	1
GASTEROSTEIFORMES		Chaenopsidae	
Aulostomatidae		*Acanthemblemaria greenfieldi*, MPM 24876, 30.4	1
Aulostomus maculatus, MPM 25182, 174.2	0	*A. aspera*, MPM 29983, 24.7	1
Aulorhynchidae		*Emblemaria pandionis*, BMNH 1938.2.2:2, 39.3	1
Aulorhynchus flavidus, AMNH 58939, 123.0	0	*Stathmonotus gymnodermis*, MPM 24881, 23.6	1
Gasterosteidae		*S. stahli*, BMNH 1939.5.12:183–189, 18.8	1
Culaea inconstans, MPM 26675, 50.2	0	Clinidae	
Gasterosteus aculeatus, AMNH 37959, 54.0	0	*Clinoporus biporosus*, BMNH 1935.4.29:1–8, 89.5	1
Macrorhamphosidae		*Clinus cottoides*, BMNH 1887.4.16:3–5, 93.0	1
Macrorhamphosus scolopax, AMNH 84458, 85.5	0	Dactyloscopidae	
MUGILIFORMES		*Dactyloscopus tridigitatus*, MPM 24981, 60.0	1
Mugilidae		*Gillellus uranidea*, MPM 30131, 29.5	1
Agonostomus monticola, MPM 13806, 41.0	0	Labrisomidae	
Mugil cephalus, USNM 152118, 93.2	0	*Labrisomus bucciferus*, MPM 31163, 57.0	1
M. curema, MPM 6817, 56.4	0	*L. nuchipinnis*, MPM 18253, 82.0	1
ATHERINIFORMES		*Malacoctenus gilli*, MPM 24947, 49.1	1
Atherinidae		*M. versicolor*, MPM 22469, 36.0	1
Atherinomorus stipes, MPM 30102, 53.4	0	*M. zonifer*, BMNH 1861.8.13:33, 47.3	1
Menidia beryllina, MPM 30404, 63.0	0	*Paraclinus fasciatus*, MPM 25004, 36.2	1
CYPRINODONTIFORMES		*Starksia lepicoelia*, MPM 29994, 23.5	1
Cyprinodontidae		Tripterygiidae	
Cyprinodon variegatus, MPM 28940, 45.6	0	*Enneanectes atrorus*, MPM 30216, 21.0	1
Fundulidae		*E. boehlkei*, MPM 11572, 18.2	1
Fundulus catenatus, MPM 15271, 70.8	0	*E. pectoralis*, MPM 22463, 26.5	1
		Lepidoblennius haplodactylus, BMNH 1890.9.23, 63.6	1

Taxon, Catalogue No., SL (mm)	Type
Callionymoidei	
Callionymidae	
Synchiropus splendidus, MPM uncat., 59.2	2
Gobiesocidae	
Gobiesox strumosus, AMNH 86887, 58.5	0
Carangoidei	
Carangidae	
Caranx latus, MPM 13771, 119.0	0
Oligoplites saurus, MPM 6364, 77.2	0
Selene vomer, MPM 2273, 75.1	0
Trachinotus rhodopus, MPM 6369, 107.0	0
Nematistiidae	
Nematistius pectoralis, MPM 6367, 215.0	0
Cirrhitoidei	
Aplodactylidae	
Aplodactylus punctatus, USNM 227298, 58.0	1
Cheilodactylidae	
Cheilodactylus variegatus, USNM 77574, 58.0	1
C. zonatus, USNM uncat., 73.5	1
Chironemidae	
Chironemus marmoratus, ROM 40360, 125.4	1
Cirrhitidae	
Amblycirrhitus bimacula, MPM 13509, 56.9	2
Cirrhitichthys oxycephalus, ROM 60291, 55.2	1
Cirrhitops hubbardi, ROM 59830, 64.5	2
Cirrhitus pinnulatus, ROM 47702, 101.0	2
Neocirrhitus armatus, ROM 59838, 44.1	1
Paracirrhites arcatus, MPM 13587, 66.7	1
Gobioidei	
Butidae	
Butis amboinensis, MPM uncat., 57.2	0
Eleotrididae	
Eleotris pisonis, USNM 314448, 77.5	0
Gobiidae	
Awaous taiasica, MPM 6811, 92.1	0
Bathygobius soporator, MPM 18232, 80.0	0
Odontobutidae	
Micropercops sp., AMNH 10441, 44.4	0
Xenisthmidae	
Xenisthmus balius, USNM 326758, 26.1	0
Labroidei	
Cichlidae	
Cichlasoma salvini, MPM 22851, 48.8	0
Etroplus suratensis, USNM 301169, 69.5	0
Embiotocidae	
Rhacochilus argyrosomus, USNM 53969, 45.7	0
Labridae	
Bodianus bilunulatus, MPM 13518, 76.3	0
B. diana, USNM 232355, 52.0	0
Cheilinus oxycephalus, USNM 262088, 62.1	2
Cheilio inermis, MPM 13369, 88.6	2
Choerodon graphicus, USNM 218548, 60.2	0
Coris variegata, USNM uncat., 86.0	2
Halichoeres bivitattus, MPM 8524, 73.6	2
Hemipteronotus martinicensis, USNM 37075, 85.0	2
Labroides dimidiatus, MPM uncat., 51.7	2
Sparisoma rubripinnis, MPM 30040, 62.6	2
Tautoga onitis, USNM 118352, 53.2	0
Thalassoma duperryi, MPM 13403, 77.7	2
T. lutescens, USNM 112696, 82.0	2
Pomacentridae	
Abudefduf saxatilis, USNM 275040, 63.5	0
Amphiprion melanopus, USNM 309519, 68.0	0
Lepidozygus tapeinosoma, USNM 275893, 51.5	0
Notothenioidei	
Nototheniidae	
Notothenia sima, AMNH 5003, 82.5	2

Taxon, Catalogue No., SL (mm)	Type
Percoidei	
Acropomatidae	
Malakichthys griseus, USNM 184143, 60.2	0
Ambassidae	
Ambassis sp., USNM 223376, 37.8	0
Chanda ranga, BMNH 1938.12.22:132–141, 40.0	0
Apogonidae	
Apogon angustatus, USNM 261750, 57.0	1
Apogonichthys ocellatus, AMNH 33808, 43.0	1
Cheilodipterus macrodon, AMNH 33714, 68.0	1
Bathyclupeidae	
Bathyclupea malayana,BMNH 1982.9.6:106–107, 117.0	0
Callanthiidae	
Callanthias australis, AMS I.18709–002, 88.0	0
C. platei, USNM 307594, 93.0	0
Caproidae	
Antigonia eos, MPM 13598, 71.3	0
Capros aper, BMNH 1963.5.14:230–239, 43.5	0
Centrarchidae	
Lepomis gibbosus, MPM 28675, 56.2	0
Micropterus salmoides, MPM 20246, 62.2	0
Centrogeniidae	
Centrogenys vaigensis, USNM 245612, 70.0	1
Centropomidae	
Centropomus armatus, USNM uncat., 108.7	0
C. ensiferus, ROM 61657, 47.7	0
C. pectinatus, ROM 61664, 61.0	0
C. undecimalis, ROM 40904, 118.5	0
Cepolidae	
Cepola rubescens, BMNH 1970.4.18:3, 438.0	2
Owstonia totomiensis, BMNH 1986.10.6:61, 91.0	2
Chaetodontidae	
Chaetodon multicinctus, MPM 13556, 89.7	0
C. miliaris, MPM 13466, 56.0	0
Datnioides quadrifasciatus, USNM 297256, 120.0	0
Dinolestidae	
Dinolestes lewinii, USNM 59932, 138.5	0
Enoplosidae	
Enoplosus armatus, USNM 48808, 77.5	0
Gerreidae	
Eucinostomus gula, USNM 43216, 45.0	0
Glaucosomatidae	
Glaucosoma scapulare, AMS I.27325–002, 45.1	0
Grammatidae	
Gramma linki, AMNH 35776, 36.3	1
G. loreto, MPM 15612, 50.4	1
Lipogramma anabantoides, AMNH 33061, 16.8	1
L. trilineata, FMNH 95658, 24.2	1
Haemulidae	
Anisotremus scapularis, USNM 127982, 55.8	1
Conodon nobilis, MPM 13778, 104.5	1
Haemulon aurolineatum, MPM 23228, 64.2	1
Hapalogenys sp., BMNH 1984.1.13:76–82, 55.0	0
Hemilutjanus microphthalmus, USNM 77623, 138.0	0
Kuhliidae	
Kuhlia rupestris, USNM 184110, 82.0	0
Kurtidae	
Kurtus gulliveri, USNM 217310, 128.0	0
Kyphosidae	
Girella tricuspidata, USNM 269547, 99.5	0
Sectator oxyurus, USNM 288880, 75.1	0
Lactariidae	
Lactarius delicatulus, BMNH 1895.2.28:51, 87.0	0
Lateolabrax japonicus, USNM 64630, 87.0	0
Latidae	
Lates albertianus, ROM 26537, 141.1	1
L. calcarifer, BMNH 1898.12.24:2, 113.5	1
L. mariae, ROM 28140, 125.2	1
L. niloticus, BMNH 1907.12.2:2959–2968, 48.5	1

Taxon, Catalogue No., SL (mm)	Type
Psammoperca waigiensis, BMNH 1933.3.11:312, 118.0	1
Lethrinidae	
Lethrinus lentjan, BMNH 1932.7.29:82–83, 70.8	0
Lobotidae	
Lobotes surinamensis, USNM 156452, 46.6	0
Lutjanidae	
Lutjanus griseus, MPM 8542, 48.1	0
L. kasmira, USNM 183109, 98.8	0
Malacanthidae	
Caulolatilus affinis, USNM 211424, 104.5	0
Monodactylidae	
Monodactylus argenteus, MPM 31026, 33.2	0
Moronidae	
Dicentrarchus labrax, BMNH 1987.2.22:1–12, 42.5	0
Morone chrysops, MPM 4569, 78.3	0
Mullidae	
Mulloidichthys martinicus, MPM 5321, 86.0	3
Parupeneus multifasciatus, MPM 13530, 79.0	3
Upeneus maculatus, USNM 126150, 76.0	3
Nemipteridae	
Pentapodus porosus, BMNH 1984.8.20:27, 62.0	0
Notograptidae	
Notograptus sp., USNM 173797, 174.0	2
Opistognathidae	
Opistognathus maxillosus, MPM 30098, 98.3	2
Oplegnathidae	
Oplegnathus fasciatus, BMNH 1905.6.6:154–161, 126.0	0
Ostracoberycidae	
Ostracoberyx sp., USNM 307282, 83.0	0
Pempherididae	
Parapriacanthus ransonneti, MPM 31028, 58.2	0
Pempheris schomburgki, FMNH 93774, 52.3	0
Percichthyidae	
Percichthys altispinnis, USNM 163382, 70.1	0
Percilia gillissi, USNM 84341, 60.0	0
Percidae	
Etheostoma nigrum, MPM 22420, 56.3	1
Perca flavescens, MPM 25409, 79.0	1
Percina maculata, MPM 20880, 76.7	1
Stizostedion canadense, MPM 6015, 86.7	1
Pholidichthyidae	
Pholidichthys leucotaenia, USNM 289924, 77.0	2
Plesiopidae	
Acanthoclinus fuscus, USNM uncat., 77.7	2
Assessor macneilli, USNM 295659, 40.5	0
Belonepterygion fasciolatum, USNM 273813, 34.0	0
Calloplesiops altivelis, USNM 261333, 60.4	0
Plesiops coeruleolineatus, USNM uncat., 45.5	0
Trachinops taeniatus, USNM 274580, 37.2	0
Polynemidae	
Polydactylus approximans, USNM uncat., 60.2	0
Polyprionidae	
Polyprion americanus, BMNH 1845.6.22:11, 190.0	0
Pomacanthidae	
Centropyge bispinosus, USNM 259696, 61.5	0
Pomatomidae	
Pomatomus saltatrix, BMNH 1967.2.1:80–85, 74.7	0
Priacanthidae	
Priacanthus hamrur, USNM 289285, 72.5	0
Pseudochromidae	
Haliophis guttatus, USNM uncat., 137.5	2
Labracinus cyclophthalmus, USNM 309335, 85.8	2
Ogilbyina queenslandiae, USNM 290792, 59.3	2
O. salvati, USNM 278149, 50.3	2
Pseudochromis elongatus, USNM 290784, 35.6	2
P. fuscus, USNM 290345, 56.5	2
'Pseudochromis' diadema, USNM 290591, 32.9	2
Sciaenidae	
Aplodinotus grunniens, MPM 16805, 66.4	0

Taxon, Catalogue No., SL (mm)	Type
Bairdiella chrysura, MPM 8954, 100.0	2
Cynoscion regalis, MPM 8969, 94.9	2
Equetus acuminatus, MPM 8522, 90.1	2
Leiostomus xanthurus, MPM 8934, 87.1	0
Menticirrhus littoralis, MPM 8443, 68.7	2
Micropogonias undulatus, USNM 142675, 67.5	0
Sciaenops ocellata, MPM 30424, 61.5	2
Stellifer lanceolatus, MPM 8936, 57.9	2
Serranidae	
Alphestes afer, USNM 235696, 89.0	1
Anyperodon leucogrammus, USNM uncat, 103.5	1
Centropristis philadelphicus, USNM 142813, 75.8	1
Chelidoperca sp., USNM 322386, 80.0	1
Diplectrum macropoma, USNM 211397, 129.0	1
Epinephelus merra, USNM 309689, 75.5	1
Grammistes sexlineatus, USNM 166994, 62.0	1
Hypoplectrodes sp., USNM 198811, 67.5	1
H. maccullochi, USNM 42039, 102.1	1
Hypoplectrus puella, MPM 23461, 92.3	1
Liopropoma rubre, MPM 25083, 41.0	1
L. sp.,USNM 322359, 76.5	1
Mycteroperca florida, USNM 176238, 59.7	1
Niphon spinosus, USNM 59739, 130.0	1
Paralabrax clathratus, USNM 54807, 53.0	1
Plectranthias nanus, USNM 288812, 24.9	1
Pseudanthias taeniatus, USNM 279782, 54.5	1
P. thompsoni, USNM uncat., 118.0	1
Pseudogramma sp., USNM 245340, 42.8	1
Serranus hepatus, USNM uncat., 73.0	1
S. tigrinus, MPM 30183, 58.3	1
Sillaginidae	
Sillago cilliata, USNM 207647, 72.6	2
Sinipercidae	
Coreoperca kawamebari, USNM 71331, 32.3	2
Siniperca chautsi, USNM 87082, 93.2	2
Sparidae	
Diplodus bermudensis, MPM 18228, 76.5	0
Symphysanodontidae	
Symphysanodon berryi, USNM 289922, 85.5	0
Synagrops bella, USNM 156955, 75.5	2
Terapontidae	
Terapon jarbua, USNM uncat., 80.0	0
Toxotidae	
Toxotes jaculator, USNM uncat., 45.0	0
Scombroidei	
Scombridae	
Scomber japonicus, AMNH 74945, 149.0	0
Sphyraenidae	
Sphyraena barracuda, MPM 11496, 93.0	0
Trichiuridae	
Trichiurus lepturus, MPM 8430, 316.0	0
Scorpaenoidei	
Agonidae	
Agonus decagonus, USNM 165146, 132.5	1
Anoplopomatidae	
Anoplopoma fimbriata, USNM 208296, 123.0	1
Aploactinidae	
Aploactis milesii, USNM 59980, 121.0	1
Bathylutichthyidae	
Bathylutichthys taranetzi, BMNH 1994.7.22:1, 100.5	0
Caracanthidae	
Caracanthus maculatus, USNM 140990, 34.5	1
Congiopodidae	
Alertichthys blacki, USNM 318386, 80.0	1
Cottidae	
Ascelichthys rhodorus, BMNH 1881.3.22:57–63, 50.0	1
Centrodermichthys analis, BMNH 1890.11.15:105, 56.7	1
Cottus bairdi, MPM 5878, 70.8	1

Taxon, Catalogue No., SL (mm)	Type
C. perplexus, USNM 258839, 51.5	1
Icelus hamatus, BMNH 1877.5.13:7–9, 60.3	1
Myoxocephalus scorpis, BMNH 1981.2.10:629, 50.5	1
Taurulus bubalis, BMNH 1981.2.20:776–794, 38.5	1
Cottocomephoridae	
Cottocomephorus grewingkii, USNM 222075, 100.0	1
Cyclopteridae	
Cyclopterus lumpus, USNM 197582, 83.8	1
Hoplichthyidae	
Hoplichthys langsdorfi, USNM 309447, 123.0	1
Liparididae	
Liparis agassizii, USNM 74697, 117.5	1
L. liparis, BMNH 1971.2.16:1757–1760, 99.5	1
Paraliparis hystrix, BMNH 1992.10.20:43–48, 87.8	1
Normanichthyidae	
Normanichthys crockeri, USNM 176507, 56.7	1
Pataecidae	
Aetapcus maculatus, BMNH uncat., 118.0	1
Pataecus fronto, BMNH 1914.8.20:282, 159.0	1
Platycephalidae	
Thysanophrys japonica, USNM 70735, 119.0	1
Psychrolutidae	
Cottunculus microps, BMNH 1981.3.16:550–553, 87.5	1
Psychrolues zebra, BMNH 1986.7.12:193, 41.5	1
Scorpaenidae	
Pterois radiata, USNM 140491, 64.8	1
Scorpaena sonorae, USNM 59463, 67.6	1
Sebastes alutus, USNM 72461, 80.0	1
Triglidae	
Bellator militaris, USNM 114793, 83.0	1
Stromateoidei	
Stromateidae	
Peprilus burti, MPM 8291, 92.4	0
Trachinoidei	
Ammodytidae	
Ammodytes americanus, AMNH 36780, 72.0	0
A. hexapterus, FMNH 80613, 106.0	0
A. lanceolatus, FMNH 34257, 177.0	0
A. personatus, USNM 104499, 86.0	0
Champsodontidae	
Champsodon sp., USNM 150556, 64.2	1
Cheimarrhichthyidae	
Cheimarrichthys fosteri, AMNH 98274, 71.0	1
Chiasmodontidae	
Chiasmodon sp., USNM 186139, 110.0	0
Dysalotus alcocki, MCZ 60806, 112.0	0

| Taxon, Catalogue No., SL (mm)	Type
Kali normani, USNM 207614, 159.6	0
Pseudoscopelus sp., ARC 8706465, 57.0	0
Creediidae	
Crystallodytes cookei, FMNH 63619, 41.0	2
Limnichthys fasciatus, AMNH 57282, 45.5	2
Percophidae	
Bembrops anatirostris, AMNH 83323, 170.0	2
B. gobioides, FMNH 67070, 112.0	2
Pinguipedidae	
Parapercis cephalopunctatus, FMNH 72471, 108.0	2
P. montillai, AMNH 50585, 94.0	2
Uranoscopidae	
Kathetostoma albiguttata, FMNH 45246, 99.0	2
Uranoscopus sp., USNM 113145, 80.0	2
Zoarcoidei	
Anarhichadidae	
Anarrhichthys ocellatus, USNM 57832, 585.0	2
Bathymasteridae	
Bathymaster signatus, USNM 24004, 130.0	2
Ronquilus jordani, MPM 394, 133.1	2
Stichaeidae	
Anoplarchus purpurescens, MPM 366, 94.2	2
Zoarcidae	
Lycodopsis pacifica, MPM 408, 117.3	2
PLEURONECTIFORMES	
Achiridae	
Achirus lineatus, MPM 13783, 95.0	0
Bothidae	
Bothus lunatus, MPM 24885, 114.0	0
Cynoglossidae	
Symphurus plagiusa, MPM 10525, 113.0	0
Paralichthyidae	
Citharichthys spilopterus, MPM 8951, 103.0	0
Pleuronectinae	
Pseudopleuronectes americanus, AMNH 33401, 119.5	0
Psettodidae	
Psettodes erumei, BMNH 1904.5.25: 197–8, 83.4	0
Poecilopsettinae	
Poecilopsetta hawaiiensis, MPM 13604, 106.3	0
Samarinae	
Samariscus triocellata, MPM 13387, 67.0	0
TETRAODONTIFORMES	
Balistidae	
Rhinecanthus aculeatus, AMNH 50748, 52.5	2
Monacanthidae	
Pervagor spilosoma, MPM 13528, 78.4	2

ing on to no other pterygiophores, but becoming continuous with the *supracarinalis posterior*. With such minimal fibre sharing of this elongate separate slip with the epaxial, it appears that the separate slip is likely to be a modified *supracarinalis posterior* or *supracarinalis medius*. Although no other taxon was found exhibiting this morphology, a few taxa do have a tendon extending to the *supracaranalis posterior* from the last fibres of the epaxial section that inserts on to the pterygiophores. We observed this condition in the cirrhitid *Paracirrhites arcatus*, some labrids (including *Sparisoma* and *Halichoeres*), as well as some blennioids. This tendon can be difficult to detect, and could be present in other taxa, although no trace of this feature was found in serranids or scorpaeniforms.

DISCUSSION

The insertion of epaxial muscle on to dorsal-fin pterygiophores is more widespread and exhibits more variation than has been previously reported. The distribution of the various recognized morphotypes suggests that it could have some value for estimating phylogenetic relationships. The most commonly encountered morphology among acanthomorphs, that of no epaxial insertions to dorsal posterolateral processes of dorsal-fin pterygiophores (Type 0), appears to be the primitive condition, as it occurs in all basal acanthomorph taxa (sensu Johnson & Patterson, 1993). Dorsal epaxial/pterygiophore associations are absent from groups such as lampridiforms, polymixiiforms, basal paracanthopterygians, beryciforms, and smegmamorphs, as well as pleuronectiforms (Table 1). Hence, Types 1–3 are apomorphic at some level.
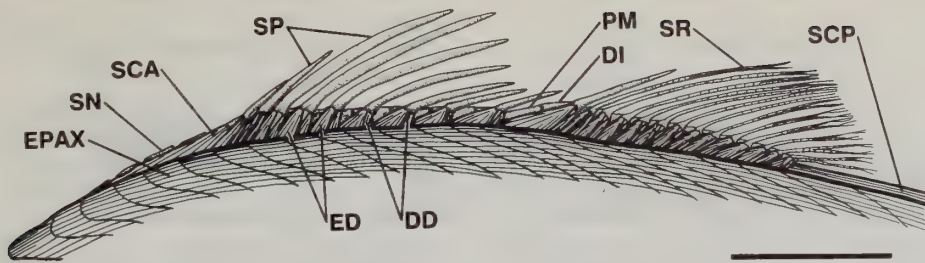
Fig. 1 Type 0 epaxial muscle as exemplified by *Morone chrysops* (MPM 4569, 78.8 mm SL). *Inclinatores dorsales* removed to expose medial muscles. Note that there is no insertion of the epaxial musculature to the distal tips of the pterygiophores. Margins of muscle demarcated by thicker lines; bone stippled. DD, *depressores dorsales*; DI, distal radial; ED, *erectores dorsales*; EPAX, *epaxialis*; PM, proximal-middle radial; SCA, *supracarinalis anterior*; SCP, *supracarinalis posterior*; SN, supraneural; SP, spines; SR, segmented ray. Scale bar = 10 mm.
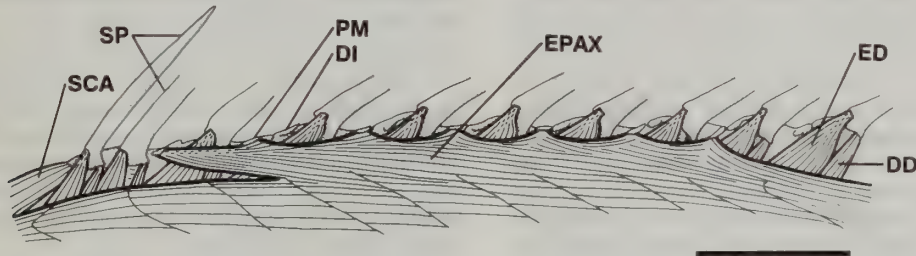
Fig. 2 Type 1 epaxial muscle as exemplified by *Epinephelus merra* (USNM 246689, 96.5 mm SL). *Inclinatores dorsales* removed to expose medial muscles. Note the separate slip of epaxial muscle which inserts dorsally on to the second pterygiophore (directly behind the second spine) and the additional insertions on to pterygiophores 3–8. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

Among these apomorphic morphologies, Type 1 is the easiest to characterize and identify. It is found among a restricted group of perciform families and is considered the exclusive epaxial/pterygiophore association of the Scorpaeniformes (see below for discussion of Type 0 condition in *Bathylutichthys*). A scorpaeniform sister group has remained elusive and this has been a serious barrier to understanding internal relationships of the Scorpaeniformes. The presence of a derived Type 1 epaxial morphology in the Scorpaeniformes and a small subset of the Perciformes suggests that the sister group of the Scorpaeniformes possibly lies within this subset. Percoid taxa rarely have been considered candidates for such status, although seven percoid families exhibit a Type 1 morphology (Table 1; Figs 2, 4–5). Despite generally being recognized as a heterogeneous and probably non-monophyletic assemblage (e.g. Johnson, 1984), percoids have been referred to as a single, identifiable taxonomic
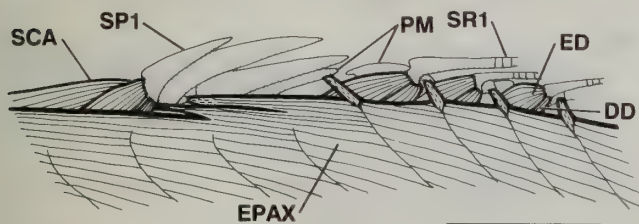
Fig. 3 Type 1 epaxial musculature in the batrachoidid *Opsanus beta* (MPM 8919, 139.5 mm SL). Insertions to the 11th dorsal-fin pterygiophore. SP1, first spine; SR1, first segmented ray; other abbreviations and methods of presentation as in Fig. 1. Scale bar = 10 mm.
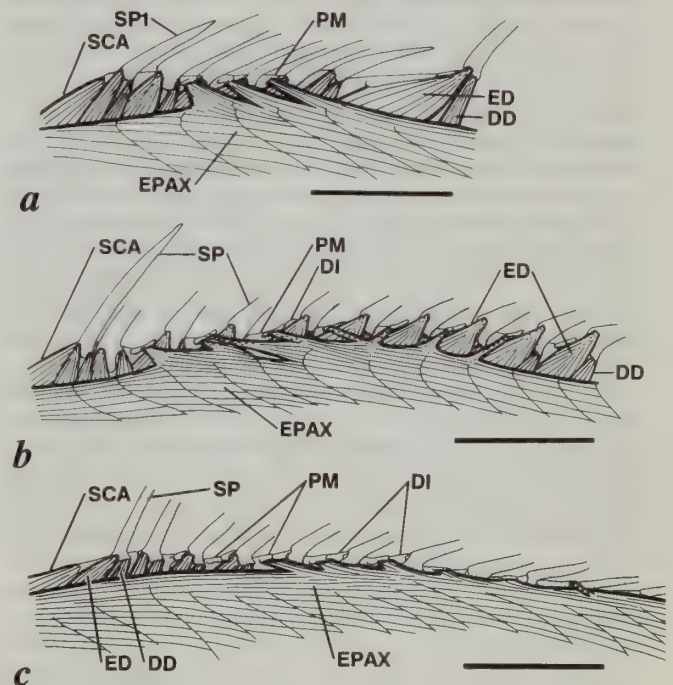
Fig. 4 Type 1 epaxial musculature in three percoids: *a*, *Apogon maculatus* (MPM 24869, 64.6 mm SL), Apogonidae, with insertions to the first through third pterygiophores; *b*, *Centrogenys vaigiensis* (USNM 150792, 53.4 mm SL), Centrogeniidae, with insertions to the first through seventh pterygiophores; *c*, *Perca flavescens* (MPM 25409, 79.2 mm SL), Percidae, with insertions to the fourth through ninth pterygiophores. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.
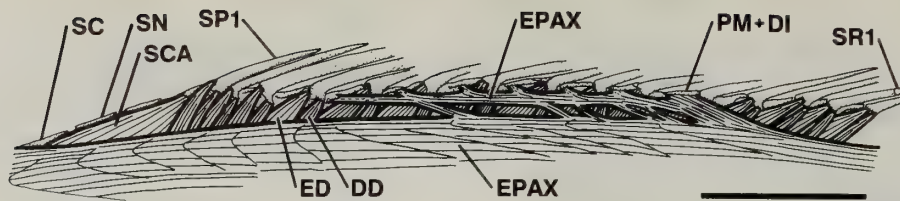
Fig. 5 Type 1 epaxial morphology with extreme fibre separation from the main epaxial body of the epaxial muscle slip inserting on to pterygiophores in *Haemulon aurolineatum* (MPM 23228, 64.2 mm SL). SP1, first dorsal-fin spine; SR1, first segmented dorsal-fin ray; other abbreviation and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

group for so long that they have been reified; in practice, most systematists regard the Percoidei as a bona fide taxon. As a consequence ichthyologists have rarely examined taxa from among the Percoidei as potential relatives of non-percoid taxa (exceptions include Johnson, 1984, 1986, 1993; Tyler *et al.* 1989), and few characters have been identified to suggest a relationship among percoids and scorpaeniforms, at least in part because few researchers have looked. These same problems apply to the more inclusive Perciformes, for which no satisfactory definition exists and membership is often questionable; families considered perciforms are rarely examined as either sister taxa or possible members of other acanthomorph orders (although see Johnson & Patterson, 1993) because, in practice, the Perciformes is treated as a monophyletic taxon.

Several additional characters suggest that a relationship between scorpaeniforms and at least some of the 'percoids' with a Type 1 epaxial morphology is worthy of consideration. For example, some larval serranids (particularly anthiines) bear at least a superficial resemblance to larval scorpaeniforms, with suspensorial and cranial bones highly ornamented by spines and ridges (cf. Figs and descriptions in: Baldwin, 1990; Johnson, 1984; Kendall, 1984; Washington *et al.*, 1984). Moreover, the general physiognomies of many adult serranids bear striking resemblances to certain scorpaeniforms. Although general similarities do not provide the necessary evidence for relationship, they hint that there might be more evidence than shared epaxial morphology; we feel it is premature to dismiss these similarities as being due to convergence before relationships are better understood.

The occurrence of Type 1 epaxial morphology in few non-percoid perciform taxa (blennioids, some cirrhitoids and some trachinoids) suggests that these should also be included in a search for a scorpaeniform sister group, or considered for inclusion among scorpaeniforms (Mooi & Johnson, in prep). For example, blennioids also resemble scorpaeniforms in having the supratemporal sensory canal enclosed by the parietal (except in most tripterygiids where the cephalic sensory canals are incompletely enclosed by bone; Springer, 1993:487 and pers. obs.). This condition is found in several other perciform taxa, including at least some zoarcoids (sensu Anderson, 1984; Travers, 1984b; all 'zoarceoids' according to Gosline, 1968:46), some pseudochromids (Gill, in prep.), and mastacembeloid synbranchiforms (Travers, 1984a), but these taxa do not have a Type 1 epaxial morphology. Champsodontids more closely resemble scorpaeniforms in having a serrate ridge overlying the canal (Johnson, 1993:14; Mooi & Johnson, in prep.), as well as Type 1 epaxials. Although blennioid parietals lack the serrate ridge or spine over the canal, the possibility of a blennioid/scorpaeniform relation-

ship deserves further study. Certain cottoids closely resemble blennioids in dorsal gill arch morphology, notably in lacking an interarcual cartilage, and in having only a single infrapharyngobranchial (infrapharyngobranchial 3), which articulates posteriorly with epibranchials 3 and 4 (e.g., compare cottoids in Rosen & Patterson, 1990: figs 34A, C and Yabe, 1985: figs 23, 24E with blennioids in Rosen & Patterson, 1990: figs 33A–B, 37, 38C–D and Springer, 1993: fig. 1). Members of the cottoid family Liparididae further resemble blennioids in lacking an uncinate process on epibranchial 1 (Kido, 1988: figs 12A–D).

Johnson & Patterson (1993: 591) found no evidence to indicate a 'pre-perciform' position for scorpaeniforms, and considered ranking them at the subordinal level within the perciforms, 'if only to stimulate the search for characters justifying their individuality.' We concur with Johnson & Patterson's proposal and award subordinal ranking for the Scorpaeniformes, as the Scorpaenoidei, within the Perciformes. In addition to the justification provided by Johnson & Patterson (1993), we believe this action will be a major step forward in diagnosing a monophyletic Perciformes. There is no contrary evidence for maintaining the two orders as separate, and the epaxial morphology and other evidence noted above suggests that the Perciformes is non-monophyletic without the inclusion of the Scorpaeniformes.

The almost universal occurrence of Type 1 epaxial muscles in the Scorpaenoidei has implications for its composition. It casts doubt on the inclusion of the Dactylopteridae and Bathylutichthyidae within the suborder, as neither family has insertions of epaxial muscle to dorsal-fin pterygiophores (Table 1). Johnson (1993: 7) also raised doubts about a relationship between dactylopterids and scorpaenoids based on the absence of a bone-enclosed supratemporal canal and
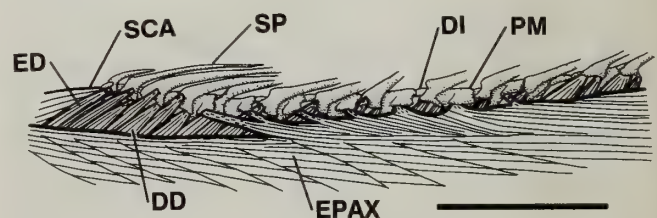

Fig. 6 Type 1 epaxial musculature in a 'primitive' scorpaeniform *Anoplopoma fimbriata* (USNM 208296, 122.2 mm SL). Note the separate slip of epaxial muscle to the third dorsal-fin pterygiophore, and other insertions of epaxial to as far posteriorly as the ninth pterygiophore. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

lack of parietal spines; Johnson & Patterson (1993: 579) considered and rejected a relationship between dactylopterids and gasterosteiforms. The monotypic family Bathylutichthyidae was recently erected by Balushkin & Voskoboynikova (1990) and placed in the Scorpaeniformes (our Scorpaenoidei) largely on the basis of trend characters variably shared with some cottoid taxa. Although *Bathylutichthys* could have secondarily lost Type 1 epaxial insertions, its position in the Scorpaenoidei should be regarded as provisional. The condition of the parietal and supratemporal canal in *Bathylutichthys* could be informative, but requires investigation.

Conversely, Mandrytsa (1991) has recently questioned the inclusion of the Pataecidae in the Scorpaenoidei (his Scorpaeniformes) based on a study of cephalic lateral-line structure. We have examined specimens of two of the three pataecid genera (*Aetapcus* and *Pataecus*; Table 1) and found that they have a typical scorpaenoid Type 1 arrangement of their epaxial musculature, corroborating their current position in the suborder. Ishida's (1994) more detailed analysis of various myological and osteological characters also conclusively nests pataecids within the Scorpaenoidei (as the sister group of the Aploactidae).

Winterbottom (1993) suggested a relationship of gobioids with the scorpaenoid family Hoplichthyidae, but this is not supported by our observations. Gobioids have no association of epaxial muscle with distal portions of the dorsal-fin pterygiophores, whereas hoplichthyids exhibit a typical scorpaenoid Type 1 pattern.

The shared Type 1 morphology in a subset of perciforms (blennioids, some cirrhitoids, Apogonidae, some Centropomidae, Centrogeniidae, Champsodontidae, Cheimarrhichthyidae, Grammatidae, Haemulidae, Percidae, and Serranidae) implies that closer relationships might exist among these taxa than are presently recognized (cf. Figs 2, 4–5, 12–17). The enigmatic family Centrogeniidae is an interesting example because its nomenclatural history reflects the possible relationships suggested by epaxial morphology. *Centrogenys vaigiensis*, the single included species, and/or its junior synonyms, has variously been classified as a scorpaeniform (e.g., Day, 1875; Fowler & Bean, 1922), a serranid (e.g., Jordan, 1923; Weber & de Beaufort, 1931; Paxton *et al.*, 1989), or has been suggested to bear a superficial resemblance to cirrhitids (Gosline, 1966; Nelson, 1984). Although *Centrogenys* does not fit comfortably into any of these taxa as they are currently diagnosed, the similar Type 1 epaxial musculature suggests that a detailed anatomical comparison could provide considerable insight into their interrelationships.

In the Centropomidae, we found that extant members of

the subfamily Latinae (*Lates*, *Psammoperca*) have a modified Type 1 epaxial morphology where the muscle insertions to the pterygiophores are separate from the main epaxial body, but are below the spine/pterygiophore articulation (Fig. 12); this arrangement could also be described as a modified Type 0 morphology with a more dorsal position of the normally proximal insertions. The Centropominae (*Centropomus*) differ in lacking such dorsal epaxial insertions to dorsal-fin pterygiophores (Type 0) (Table 1). Greenwood (1976) hypothesized the monophyly of the Centropomidae, with its two subfamilies as sister taxa, on the basis of two synapomorphies: pored lateral-line scales extending to posterior margin of caudal fin, and neural spine of second vertebra markedly expanded in an 'anteroposterior direction.' Pored lateral-line scales extend well on to the caudal fin in many acanthomorph fishes, and reach, or nearly reach, the posterior margin of the fin in several families, including sciaenids (Greenwood, 1976), moronids (G.D. Johnson, pers. comm.), most pempheridids, rhyacichthyids (Springer, 1983) and polynemids. Therefore, this character does not provide convincing evidence of relationship, and may be plesiomorphic within perciforms. We also are not convinced that Greenwood's second character (also noted by Gosline, 1966), expansion of the second neural arch, is homologous in centropomines and latines. In adult centropomines (see Fraser, 1968: 455 for discussion of ontogenetic variation), the second neural spine is broadly expanded over most of its length (resulting in a truncated or rounded distal tip to the spine) and closely applied to the first neural spine, which is narrow and sharply pointed (see Fraser, 1968: fig. 14; Greenwood, 1976: fig. 25d; Rosen, 1985: fig. 39B). In contrast, the anterior neural spine morphology of the latines does not differ markedly from the conditions found in various basal perciforms; the second neural spine is only expanded proximally, and is not closely applied to the first neural spine (see Greenwood, 1976: figs 25a-c). Given the lack of convincing synapomorphies to unite the subfamilies Latinae and Centropominae, and considering the differences in epaxial morphology (as well as various other anatomical differences listed by Greenwood, 1976), there is no justification for placing them in a single family. Based on their modified Type 1 epaxial morphology, we here remove the African/Indo-Australian genera *Lates* and *Psammoperca* from the Centropomidae to a separate family, Latidae. *Hypopterus* (Western Australia) and *Eolates* (Italy [Monte Bolca]), included as latines by Greenwood (1976), presumably also belong to the newly created Latidae. Greenwood (1976) considered *Psammoperca macroptera*, the type species of *Hypopterus*, to be a synonym of *P. waigiensis*, the single species he recognized in *Psammoperca*; however, recent authors (e.g., Allen & Swainston, 1988: 62; Paxton *et*
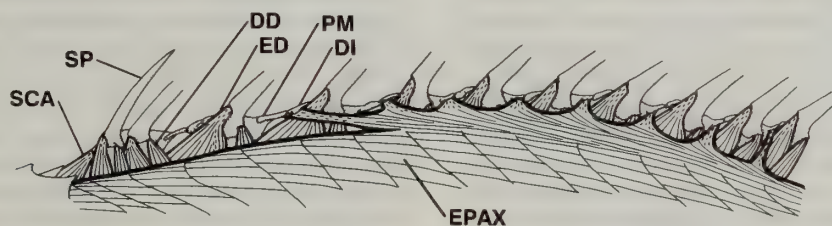
Fig. 7 Type 1 epaxial musculature in the scorpaeniform *Pterois radiata* (USNM 140493, 63.3 mm SL). Note the insertion of the epaxial muscle on to elements of the second pterygiophore and those posterior to the ninth pterygiophore. Abreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.
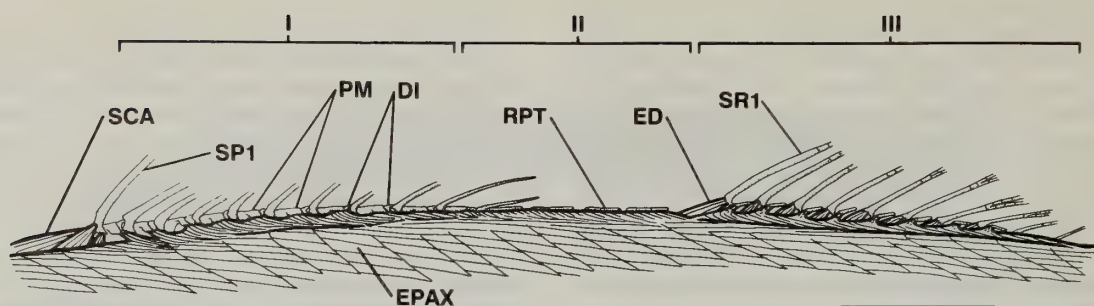
Fig. 8 An unusual Type 1 epaxial morphology in *Normanichthys crockeri* (USNM 176507, 63.4 mm SL). I – portion of the epaxial that inserts on to the anterior pterygiophores largely separate from the main body of the epaxial, with only a few fibres shared from each myoseptal section. The exceptions are the insertions on the two anteriormost pterygiophores which have many of their fibres originating from the main epaxial muscle body. II – portion inserting on to pterygiophores that is not separate from the main epaxial body. III – portion inserting on to the ptergygiophores bearing segmented rays, is mostly separate until just beyond the last ray where it merges with the rest of the epaxial musculature. RPT, rayless pterygiophore; other abbreviations and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

al., 1989: 482) have regarded *Hypopterus* as a valid, monotypic genus. We provisionally retain the Centropomidae (*Centropomus* only) until its relationships are better understood.

The Trachinoidei as defined by Pietsch & Zabetian (1990) exhibit a variety of epaxial morphologies (Table 1). Ammodytids and chiasmodontids have Type 0, champsodontids and cheimarrhichthyids have Type 1, and Type 2 is found in the creediids, percophidids, pinguipedids and uranoscopids. Considering the discussion by Johnson (1993: 13–15), this epaxial character distribution casts further doubt on the integrity of this suborder as currently constituted. Although it seems likely that the epaxial morphologies as defined here have evolved more than once among acanthomorphs, it is difficult to reconcile their distribution with the phylogeny provided by Pietsch & Zabetian (1990). One of their phylogenetic hypotheses is a sister group relationship between the Chiasmodontidae and the Champsodontidae. The Chiasmodontidae do not exhibit any muscle insertions on the dorsal-fin pterygiophores, whereas the Champsodontidae have a Type 1 condition very similar to that of scorpaenoids and serranids. Ammodytids, considered a derived trachinoid group, exhibit the primitive Type 0 condition, while a putative basal taxon, *Cheimarrichthys*, has Type 1, usually a derived morphology. Reversals are possible and structural homologies are uncertain (as discussed below), but the inconsistencies among these taxa suggest a more thorough investigation of the composition of the Trachinoidei sensu Pietsch & Zabetian (1990) is warranted.

There are differences even among those trachinoids that share a Type 2 morphology. *Parapercis* has a separate muscle that runs the entire length of the dorsal fin, with only intermittent epaxial fibres contributing to the muscle body. The posterior end of this separate muscle has some fibre and fascia connection with the *supracarinalis posterior* and only very weak attachments to the dorsal-fin pterygiophores that bear segmented rays. These pterygiophore insertions become strong anteriorly on spine-bearing pterygiophores, and the muscle is continuous with the *supracarinalis anterior*. This morphology is reminiscent of that of the Mullidae, described above, but shows an even closer association with the *supracarinalis* muscles, suggesting a *supracarinalis* derivation, rather than an epaxial one, for these pterygiophore insertions. This is completely different from the condition in

percophidids (*Bembrops*), which have a more typical Type 2 morphology with epaxial insertions on to the five pterygiophores of the anterior dorsal fin and to the first pterygiophore of the second, and with the anterior and posterior *supracarinalis* muscles entirely separate from the epaxial musculature. Of course, such differences can be interpreted as autapomorphies for families and genera among the trachinoids, but can also be considered suggestive of non-relationship.

Epaxial/pterygiophore associations can also strengthen hypotheses about monophyly of currently recognized groups. Although not unique among perciforms, the occurrence of the Type 1 attachment in *Niphon spinosus* (Fig. 13) and its proposed relatives, the serranids, lends support to Johnson's (1983) placement of *Niphon* within this family based on other characters. *Niphon* had previously been aligned with the Percichthyidae, a family that exhibits Type 0 epaxial morphology.

Among blennioids (sensu Springer, 1993), the Type 1 epaxial morphology has been found in all examined taxa, but there is some variation in details. Tripterygiids, dactyloscopids, clinids, chaenopsids and blenniids have a separate, more-or-less fan-shaped, anterior slip of the epaxial muscle bundle that inserts on to the distal portions of the anterior dorsal-fin pterygiophores and extends forward to the skull (Fig. 14a-c). We have not found this anterior slip elsewhere among acanthomorphs with epaxial attachments to dorsal-fin pterygiophores, and interpret it as a synapomorphy of the Blennioidei. This corroborates Springer's (1993) hypothesized monophyly of the suborder. However, labrisomids are an exception among blennioids in exhibiting a more typical Type 1 morphology, without an anterior slip to the skull (Fig. 14d). On the basis of molecular work, Stepien *et al.* (1993) hypothesized that the Labrisomidae are nested within the Blennioidei. Morphological characters provided by Springer (1993) also suggest that the Labrisomidae are not a basal blennioid family; for example, labrisomids, clinids, blenniids, and chaenopsids are more derived than tripterygiids and dactyloscopids in having the dorsalmost pectoral-fin ray articulating only with the dorsalmost proximal radial (vs with the scapula). Therefore, the absence of an anterior extension of the dorsal epaxial slip to the skull is most parsimoniously interpreted as a reversal, and a synapomorphy of the Labrisomidae.

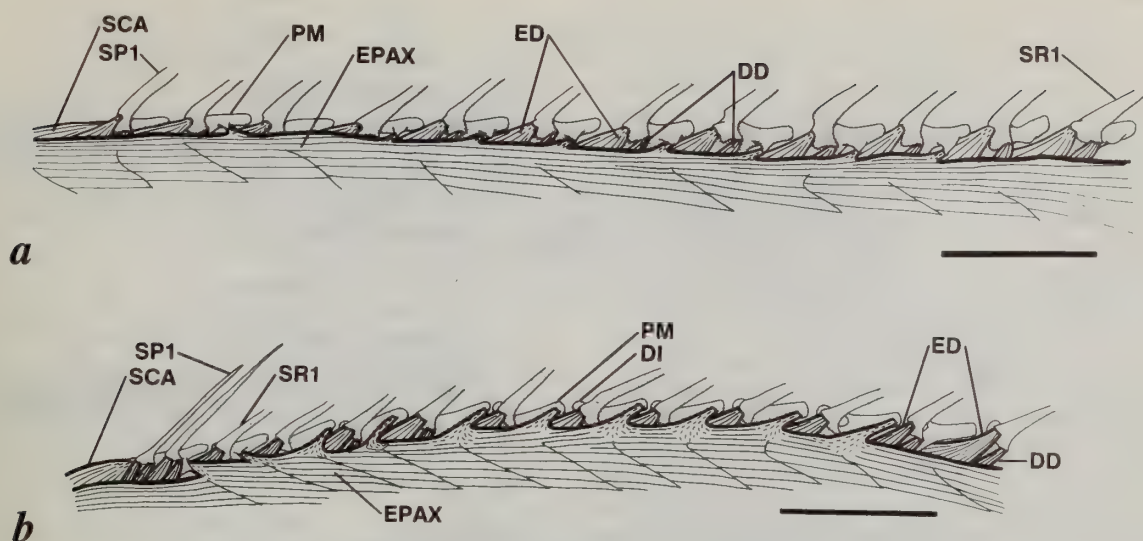It is also possible that the discovery of epaxial/

Fig. 9 Type 2 epaxial musculature as exemplified by: *a*, *Opistognathus maxilloxus* (MPM 30098, 98.3 mm SL); *b*, *Ronquilus jordani* (MPM 394, 133.1 mm SL). Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.
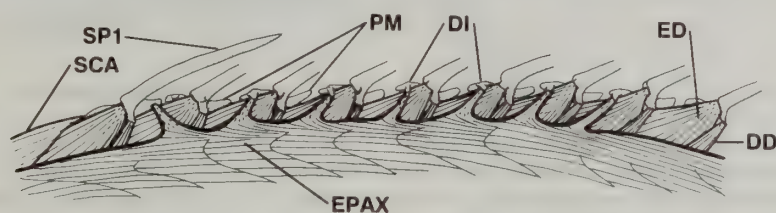

Fig. 10 Epaxial insertions via long tendons of *Sparisoma rubripinne* (MPM 30040, 62.6 mm SL), typical of some Type 2 epaxial muscles. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bar = 5 mm.
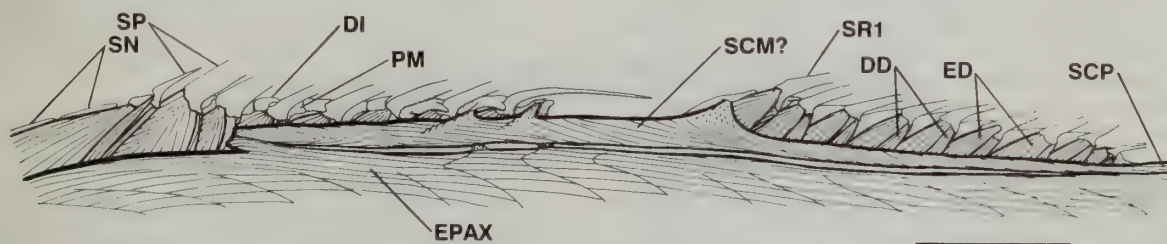

Fig. 11 Type 3 epaxial musculature as exemplified by *Parupeneus multifasciatus* (MPM 13530, 79.0 mm SL). In contrast to Types 1 and 2, the dorsal epaxial has direct fibre insertion to only one anterior pterygiophore, and ventral to the articulation with the spine. These anterior fibres merge with what is possibly a modified *supracarinalis medius* (SCM?), which has a similar anterior insertion and tendonous insertions to a few posterior pterygiophores more dorsally. The epaxial muscle shares only a few fibres with the *supracarinalis medius* near the posterior end of the first dorsal fin. The *supracarinalis medius* is contiuous with the *supracarinalis posterior*. SCM?, possible *supracarinalis medius*; other abbreviations and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

pterygiophore morphologies could help to determine the relationships of some of the *incertae sedis* genera of the Percoidei as identified by Johnson (1984: table 119). For example, *Siniperca* has Type 2 musculature, which, although a relatively common morphology, does circumscribe a smaller perciform group from which possible relationships could be initially explored. Johnson (1984) suggested a relationship between *Symphysanodon* and *Synagrops* based on larval morphology. We find the former taxon to have Type 0 and the latter to exhibit Type 2 epaxial morphologies. Although this does not refute a relationship, clearly more work needs to be done. Other orphan percoid genera such as *Lateolabrax* and *Hapalogenys* have Type 0 morphology,

which suggests they are unlikely to be included among Type 1 taxa such as the Serranidae and Haemulidae (where each genus, respectively, had been traditionally placed).

Many percoid families have not had their close relatives identified. Epaxial morphology might limit the search for possible relationships for some of these taxa. For example, the Pholidichthyidae exhibit Type 2 morphology, and their relationships might be narrowed to other taxa with this morphology. Gill & Mooi (1993) summarized evidence suggesting a possible relationship of the Notograptidae to acanthoclinine plesiopids. Notograptids and some acanthoclinines share Type 2 morphology, which is absent in other plesiopids (Table 1), and this perhaps provides additional support for
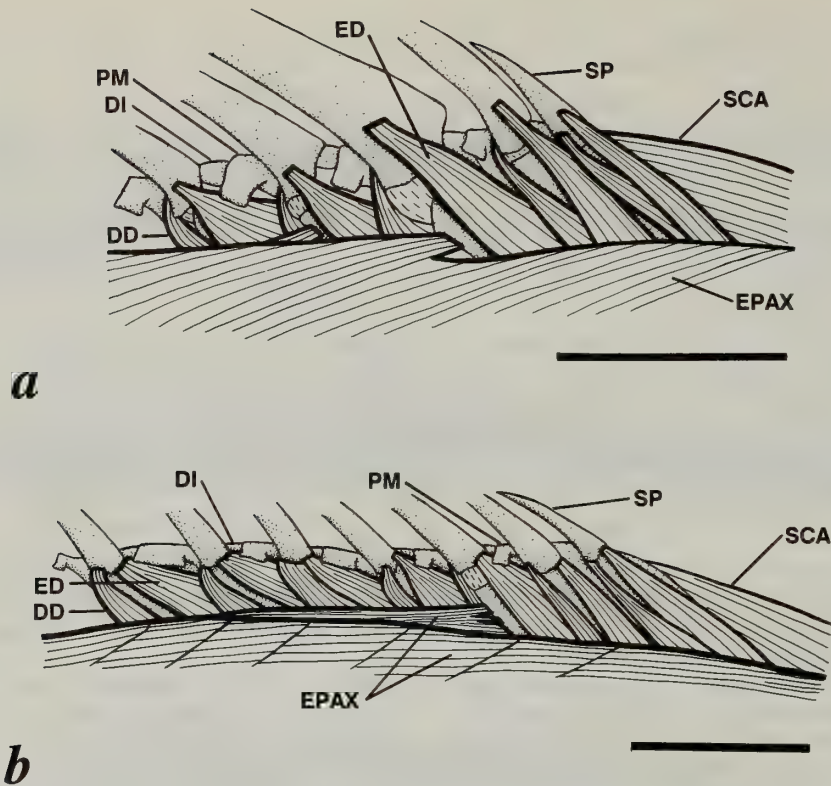
Fig. 12 Epaxial muscle morphology in: *a*, *Lates niloticus* (ROM 28524, 80.8 mm SL); *b*, *Psammoperca waigiensis* (ROM 46627, 91.2 mm SL). Note the insertions on to the second pterygiophore just ventral to the spine/pterygiophore articulation. Abbreviations and other methods of presentation as in Fig. 1. Scale bars = 5 mm.
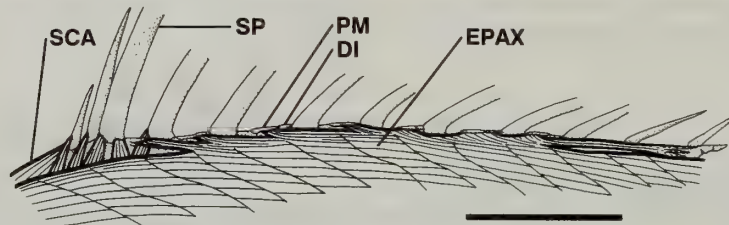
Fig. 13 Type 1 epaxial musculature in *Niphon spinosus* (USNM 59739, 128 mm SL). Note the separate slip of muscle inserting on to the second dorsal-fin pterygiophore and insertions to the 2nd through 8th pterygiophore, as in *Epinephelus* (Fig. 2). A separate bundle of fibres originates tendonously from the 10th pterygiophore to merge with those from the main epaxial muscle body. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 10 mm.

their relationship, or at least does not contradict such a conclusion.

Variation within families exhibiting a particular morphotype has considerable potential for exploring internal relationships. Among serranids, the anthiines *Hypoplectrodes*, *Acanthistius*, and *Plectranthias* all have very similar epaxial morphologies (Fig. 15), in which a short and not highly differentiated slip of muscle inserts on to the second pterygiophore, and a weak tendon extends from the myoseptum to the first pterygiophore. This differs notably from the condition in more typical anthiines, such as *Pseudanthias*, where a completely separate slip of epaxial muscle extends from below the fifth pterygiophore to insert on to the first through fourth pterygiophores (Fig. 16). These differences could provide evidence to unite members of one or another of these anthiine groups. If epinephelines are the sister group of anthiines as implied by Johnson (1988) and supported by

Baldwin & Johnson (1993), decisions concerning homology and character definition become crucial; primitive epinephelines (*Niphon*, *Epinephelus*) have a separate slip of muscle inserting on to the second pterygiophore, but no weak tendon to the first pterygiophore, a combination of features found in the two anthiine groups (cf. Figs 2, 13, 15, 16).

Variation in morphology of epaxial musculature might prove useful in other taxonomic groups. Insertion patterns of epaxial fibres to pterygiophores, the portions of the pterygiophore involved in the insertion, the degree of separation of the involved musculature from the main body of the epaxial, and the relationship of the muscle with the *supracarinalis* all vary. Among the haemulids examined, *Anisotremus* has a limited number of attachments involving only the fourth and fifth pterygiophores, *Conodon* exhibits a more robust continuous series of insertions extending from the third to seventh pterygiophores more typical of Type 1, and *Haemu-*
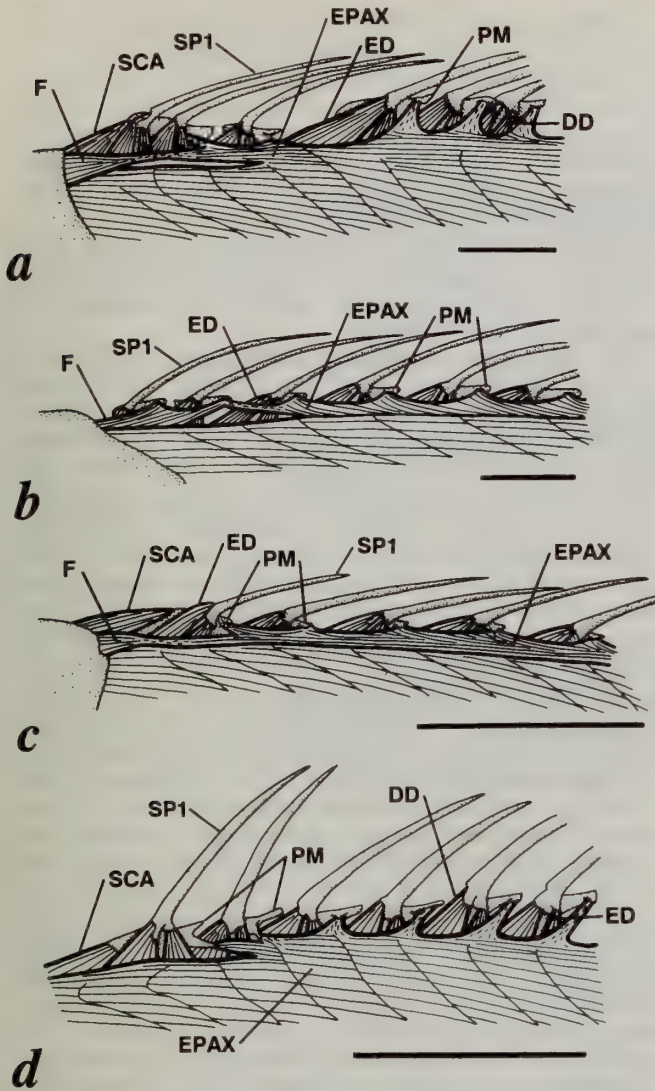
Fig. 14 Epaxial musculature of blennioids: *a*, Tripterygiidae, *Enneanectes pectoralis* (MPM 22463, 26.5 mm SL), insertions to ninth pterygiophore; *b*, Chaenopsidae, *Acanthemblemaria greenfieldi* (MPM 24876, 30.4 mm SL), insertions to 13th pterygiophore; *c*, Blenniidae, *Entomacrodus nigricans* (MPM 18256, 55.4 mm SL), insertions to 11th pterygiophore; *d*, Labrisomidae, *Labrisomus bucciferus* (MPM 31163, 57.0 mm SL), insertions to 13th pterygiophores. F, fan-shaped anterior slip of epaxial to skull; other abbreviations and methods of presentation as in Figs 1, 3. Scale bars = 1 mm (a,b), 5 mm (c,d).
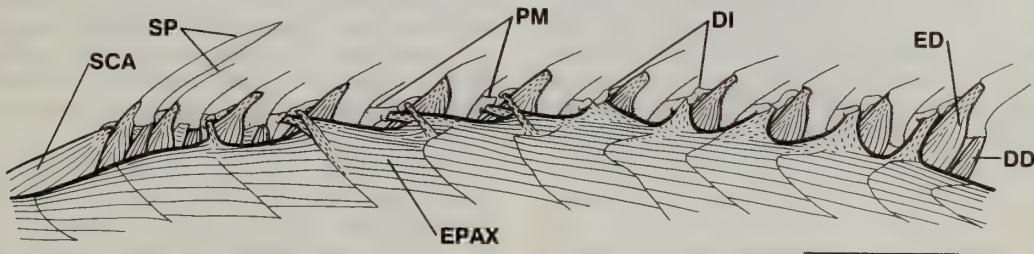
lon has an almost completely separate series of muscle fibres that insert on to the third to ninth pterygiophores (Fig. 5). Type 1 appears to be the primitive condition for the cirrhitoids (Fig. 17), with a secondary change to an epaxial/pterygiophore association resembling more closely a Type 2 morphology among some cirrhitids, which could be indicative of close relationship (Table 1). Among sciaenids both epaxial muscle Types 0 and 2 occur, although their distributions are difficult to interpret with our current understanding of sciaenid relationships (Table 1; Sasaki, 1989). Within scorpaenoids there is variation in epaxial morphology among the higher taxa. More extensive surveys within these and other groups with epaxial/pterygiophore insertions could help to elucidate some of their intrarelationships.

Basal taxa (Embiotocidae, Pomacentridae, and Cichlidae) of the suborder Labroidei (Kaufman & Liem, 1982; Stiassny & Jensen, 1987) exhibits Type 0 morphology, whereas some labrid taxa exhibit Type 2 (Table 1). It is most parsimonious to interpret Type 2 epaxial muscle as independently derived within labrids. This interpretation places *Bodianus*, *Choerodon*, and *Tautoga* as basal genera among the Labridae, and might be helpful for determining the polarization of other characters for phylogeny reconstruction in this confusing group.

Some tetraodontiforms exhibit epaxial insertions on to the distal tips of the dorsal-fin pterygiophores that resemble Type 2: Balistidae (*Rhinecanthus*, pers. obs.; probably *Balistes*, *Balistapus*, *Melichthys*, and *Odonus* from figs 78, 86, 88 and 90 in Winterbottom, 1974b), Monacanthidae (*Pervagor*, pers. obs.; probably *Aluterus*, *Cantherines*, *Chaetoderma*, *Paraluteres*, *Paramonacanthus*, and *Stephanolepis* from figs 100, 102–105 and 108 in Winterbottom, 1974b), probably Triacanthidae (*Triacanthus*, *Tripodichthys*, *Trixiphichthys* from figs 66, 76–77 in Winterbottom, 1974b), and perhaps some Triacanthodidae (*Triacanthodes*, *Tydemania*, and *Macrorhamphosodes* but not *Hollardia* or *Parahollardia* from figs 49, 57–58, 61 and 64 in Winterbottom, 1974b). Consideration of the overall anterodorsal morphology of balistids, monacanthids, and triacanthids suggests that these insertions are likely to have been derived independently of (and non-homologous with) those found in the Perciformes. In these tetraodontiforms, the anterior spinous dorsal fin is closely associated with the back of the skull and separated from the soft dorsal fin. It seems that the robust pterygiophores of the spinous dorsal fin act functionally as a supraoccipital crest and that the epaxial musculature inserts on to these elements as it would to such a crest. If triacanthodids, which possess a more conventional arrangement of spinous dorsal fin and posterior skull, do have epaxial/dorsal pterygiophore inser-

Fig. 15 Type 1 epaxial musculature in *Acanthistius sebastoides* (USNM 246689, 96.5 mm SL). A weak tendon extends from a myoseptum to the first pterygiophore and a short and not highly differentiated muscle slip inserts on to the second pterygiophore. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.
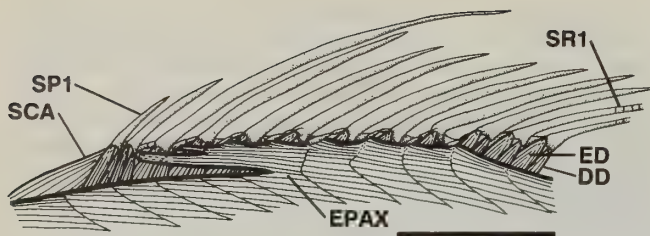
Fig. 16   Type 1 epaxial musculature in *Pseudanthias taeniatus* (USNM 279782, 44.8 mm SL). A separate slip of the epaxial inserts on to the first to fourth dorsal-fin pterygiophore, and epaxial insertions occur as far posteriorly as the eighth pterygiophore. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

tions, an argument could be made for homology with a Type 2 morphology found among the perciforms, and implied relationships should be investigated. Optimizing epaxial character distribution on existing phylogenies of the tetraodontiforms (Winterbottom, 1974b; Leis, 1984) implies that the Type 2 morphology is the primitive condition for the order. Unfortunately, the character does not provide additional evidence for intrarelationships because the remaining extant families of tetraodontiforms do not possess a spinous dorsal fin.

Even among taxa that do not exhibit epaxial insertions on to the distal portions of the proximal-middle pterygiophores or on to the distal radials, we did observe some possibly significant variation in other muscle morphology. As noted above, most (if not all) acanthomorphs have epaxial muscle insertions on to the proximal ends or along the shafts of the dorsal-fin pterygiophores. In most pleuronectiforms the epaxial muscle inserts via bundles of muscle fibres that pass underneath the *depressores dorsales*. *Psettodes*, usually considered the sister group of other pleuronectiforms, has the epaxial muscles overlying most of the length of the pterygiophores, with very short connections extending under the depressors to the pterygiophore shafts just ventral to the spine articulations. These connections only occur on the first 12 pterygiophores. *Psettodes* is the only genus with dorsal-fin spines; all other flatfishes have epaxial insertions on to a higher number of pterygiophores, although most of the examined taxa have dorsal fins extending over the head. The extent to which the epaxials overlie the pterygiophores in remaining flatfishes varies considerably and might be of interest for determining relationships. The few examined bothids, paralichthyids and samarines have the epaxials covering about half the length of the pterygiophores before short fibres attach to these bones. In available achirids the arrangement is similar to that described for bothids for the most posterior insertions, but anteriorly there are separate, elongate muscle slips that insert high on to the pterygiophore shafts just ventral to the ray articulations (Fig. 18). The cynoglossids, considered close relatives of the achirids (Chapleau, 1993), have an epaxial morphology more similar to that of *Psettodes* in the one species examined. *Poecilopsetta* (Poecilopsettinae) has epaxial muscles that lie only as far dorsally as the proximal tips of the dorsal-fin pterygiophores, a condition that appears derived among pleuronectiforms and could provide evidence for relationship if observed in other taxa. Additional taxa need to be surveyed and character definitions must be clarified before epaxial morphology can

contribute to an hypothesis of pleuronectiform phylogeny, but such an investigation appears worthy of pursuit.

A similar, though less extensive, series of epaxial insertions under the depressors is found in *Urophycis* of the Gadidae (Fig. 19). Gadoids have not been thoroughly surveyed, but variation in epaxial muscle morphology, which is relatively simple to observe, might be useful for defining broad groups among gadoids, and paracanthopterygians in general. The occurrence of a Type 1 epaxial morphology among batrachoidids also suggests that a further survey of paracanthopterygians could contribute to the understanding of relationships within this taxon.

Of course, epaxial muscle morphology is not informative in all cases. For example, the Callionymoidei have a highly modified Type 2 condition consisting of a complex series of epaxial insertions on to the pterygiophores and modified neural spines. This will not help determine whether the Callionymoidei and Gobiesocidae are sister taxa, as hypothesized by Gosline (1970) and Winterbottom (1993: 409), because the latter taxon does not have a spine-bearing dorsal fin. It would be reasonable to suggest that any epaxial muscle associated with the fin would also have disappeared or have become reduced. Like any other feature, epaxial morphology can undergo secondary loss or autapomorphic modification.

The homology of the three epaxial muscle morphotypes identified remains uncertain. It is unlikely that they form a nested set of character states. That a single morphotype can be independently derived from a Type 0 condition is illustrated by the independent development of Type 2 in some labrids, and similarly in the Acanthoclininae, a derived taxon within the Plesiopidae which otherwise exhibit Type 0 (Table 1). The occurrence of a Type 1 morphology in some paracanthopterygians, usually considered unrelated to perciforms, also indicates non-homology of the character state as recognized here. These examples suggest that the morphologies themselves require better definition. With more sophisticated inquiry through ontogenetic or neurological studies, it is possible that these cases of non-homology can be dismissed as inappropriately recognized character state equivalence. In the apparently unique morphology of the Mullidae, Type 3, the pterygiophore insertions involve both epaxial and *supracarinalis* fibres (Fig. 11). The muscle is essentially separate from the main epaxial muscle body over its entire length, a condition very different from that found in the Type 1 or 2 morphologies. It appears that the Type 3 musculature is directly derived from the *supracarinalis* muscles, rather than from the epaxial muscles. This also seems likely in the pinguipedid trachinoid *Parapercis*, where the muscle bundle inserting on to the dorsal-fin pterygiophores is continuous with the *supracarinalis anterior* and *posterior*. The condition in mullids and *Parapercis* could provide evidence that, in at least these taxa, the sheet of muscle inserting on to dorsal-fin pterygiophores is actually derived from the *supracarinalis*, and only secondarily shares muscle fibres from the *epaxialis*. These problems of homology and ontogeny of the muscle are beyond the scope of this paper.

Despite these concerns, we are confident that epaxial morphology is useful for exploring the relationships of acanthomorph taxa. Of course, this one character complex must be taken in the context of other characters before any definitive statements can be made regarding, for example, percoid/scorpaenoid relationships, or before making generalizations concerning the integrity of such groups as the trachinoids. However, one important concept that the inves-
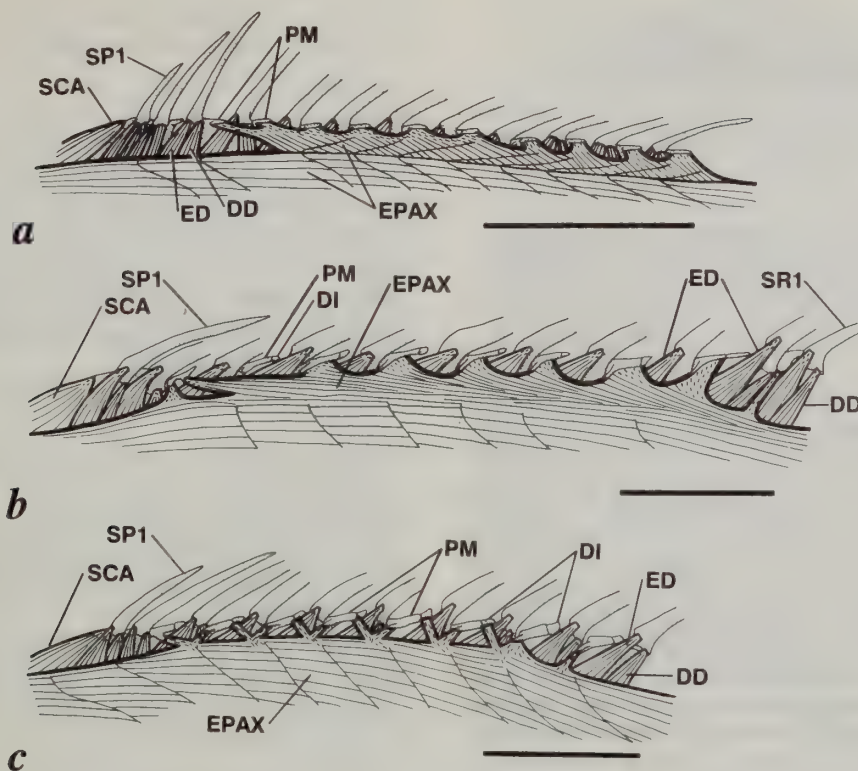
Fig. 17 Epaxial musculature in cirrhitoids: *a*, Type 1 in Aplodactylidae, *Aplodactylus punctatus* (USNM 227298, 58.0 mm SL); *b*, modified Type 1 in Cirrhitidae, *Paracirrhitus arcatus* (MPM 13587, 66.7 mm SL); *c*, Type 2 in Cirrhitidae, *Amblycirrhitus bimacula* (MPM 13509, 56.9 mm SL). Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.
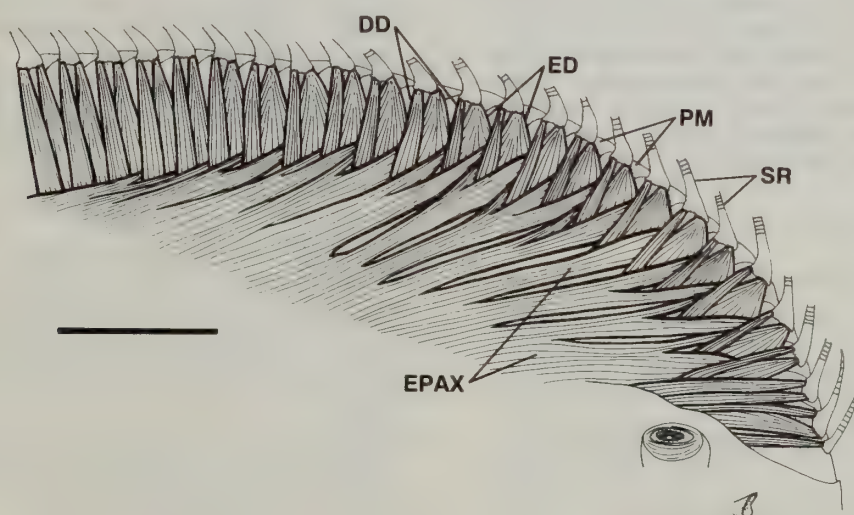
Fig. 18 Epaxial musculature of the pleuronectiform *Achirus lineatus* (MPM 13783, 95.0 mm SL). Individual slips of *epaxialis* insert on to the dorsal third of the dorsal-fin pterygiophore shafts under the *depressores dorsales*. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 10 mm.
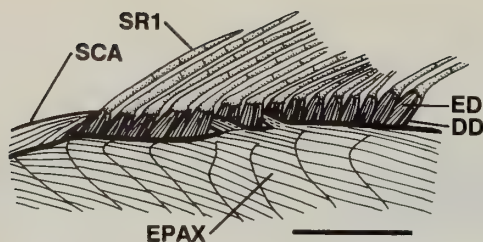
Fig. 19 Epaxial musculature in the gadid *Urophycis regia* (MPM 31175, 133.0 mm SL). Individual slips of muscle extend from the main *epaxialis* body to insert on the dorsal-fin pterygiophore shafts under the *depressores dorsales*. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.

tigation of epaxial muscle variation elucidates is the need to shrug off the straitjacket of present classifications when investigating phylogeny of higher taxa. This is particularly true when the taxa are already recognized as non-monophyletic, undefined, or poorly defined (e.g., Percoidei, Perciformes, Paracanthopterygii), but have in essence been reified over time. It is necessary to look beyond the traditional taxonomic boundaries, not only when dealing with undefined groups such as the percoids, but also when investigating apparently well-defined or well-established taxa such as the scorpaenoids and trachinoids. Epaxial muscle insertions to dorsal-fin pterygiophores provide one character complex that illustrates the potential and novel relationships that such an approach can suggest. These possible relationships await rejection or corroboration from similar studies of additional characters.

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